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Downstream Movements and Estuarine Residence by Atlantic Salmon Parr (*Salmo salar*)

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Cunjak, R. A., E. M. P. Chadwick, and M. Shears. 1989. Downstream movements and estuarine residence by Atlantic salmon parr (*Salmo salar*). Can. J. Fish. Aquat. Sci. 46: 1466–1471.

Downstream migrations and estuarine residence by Atlantic salmon (*Salmo salar*) parr and smolts were studied in a small river on the northwest coast of Newfoundland in 1983 and in 1987. There were large downstream migrations in the spring and small downstream migrations in the fall. The major differences between the two types of migrant were that parr migrated about 1 wk before smolts and at a younger age compared with smolts and while parr remained in the estuary throughout the summer, smolts did not. Modal age and mean size were less for parr sampled in the estuary compared with those sampled at the counting-fence which suggested that the smallest parr were not captured by the fence. The estuarine population of parr represented a significant proportion of the river's total production of salmon. Parr were found throughout the estuary in salinities up to 24 parts per thousand but were most abundant near the river mouth. There was evidence that larger parr became smolts and eventually migrated to sea, but smaller parr probably returned to the river for overwintering. It is clear that estuaries should be included as habitat used for rearing Atlantic salmon.

Les migrations de dévalaison et la résidence en estuaire chez les tacons et les smolts de saumon de l'Atlantique (*Salmo salar*) ont été étudiées dans un petit cours d'eau de la côte nord-ouest de Terre-Neuve en 1983 et 1987. La dévalaison était importante au printemps et faible à l'automne. Les grandes différences entre les deux types de migrants étaient que les tacons migraient environ une semaine avant les smolts, et à un âge plus jeune, et que les tacons passaient l'été dans l'estuaire alors que les smolts n'y restaient pas. L'âge modal et la taille moyenne étaient inférieurs chez les tacons échantillonnés dans l'estuaire par rapport à ceux observés à la barrière de dénombrement, ce qui semble indiquer que la barrière ne retenait pas les poissons de petite taille. La population estuarienne de tacons représentait une proportion importante de la production totale de saumon de la rivière. On a trouvé des tacons dans tout l'estuaire à des salinités allant jusqu'à 24×10^{-6} ppm, mais ils abondaient surtout près de l'embouchure de la rivière. Certaines indications montrent que les tacons de grande taille se transformaient en smolts pour ensuite partir en mer, mais les tacons de petite taille retournaient probablement passer l'hiver dans la rivière. Il est clair que les estuaires devraient être considérés comme habitat servant au grossissement du saumon de l'Atlantique.

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In Canada, the downstream movements and subsequent utilization of estuarine environments by juvenile Atlantic salmon (*Salmo salar*) have been observed in Ungava (Power 1969; Power et al. 1987), the Quebec North Shore of the Gulf of St. Lawrence (Power and Shooner 1966; Randall and Power 1979), and Newfoundland (Hutchings 1986; J. B. Dempson, Department of Fisheries and Oceans, St. John's, Newfoundland, pers. comm.). Despite the widespread occurrence of this behaviour, our appreciation of the importance of estuaries in the ecology of salmon is still limited. For example, questions pertaining to the population structure, residence times, and growth rates of estuarine populations remain unresolved.

At Western Arm Brook, in northwestern Newfoundland, a fish-counting fence near the mouth of the river has been in operation every year since 1971 (Chadwick 1987). There has been a distinct downstream movement of Atlantic salmon parr immediately preceding, but overlapping with, the smolt migration in the river (Chadwick and Leger 1986). To determine the ultimate fate of these parr, a preliminary survey was conducted in the lower river and estuary in 1983. A more detailed program of investigation into the phenomenon was initiated in 1987, and is ongoing.

In this paper, our objectives were two-fold. First, we sought to determine the population size and structure of salmon parr residing in the estuary of Western Arm Brook in relation to the river's production of salmon (i.e. smolts). Having established that the estuarine population of parr was significant, our second objective was to determine the duration of residence, general behaviour, and distribution of parr within the estuary. We present evidence that the occupation of estuarine environments by salmon parr is temporary. Further, we suggest that many of these parr are essentially presmolts that use the estuary as a transitory rearing environment prior to the completion of smoltification and out-migration in late spring or autumn.

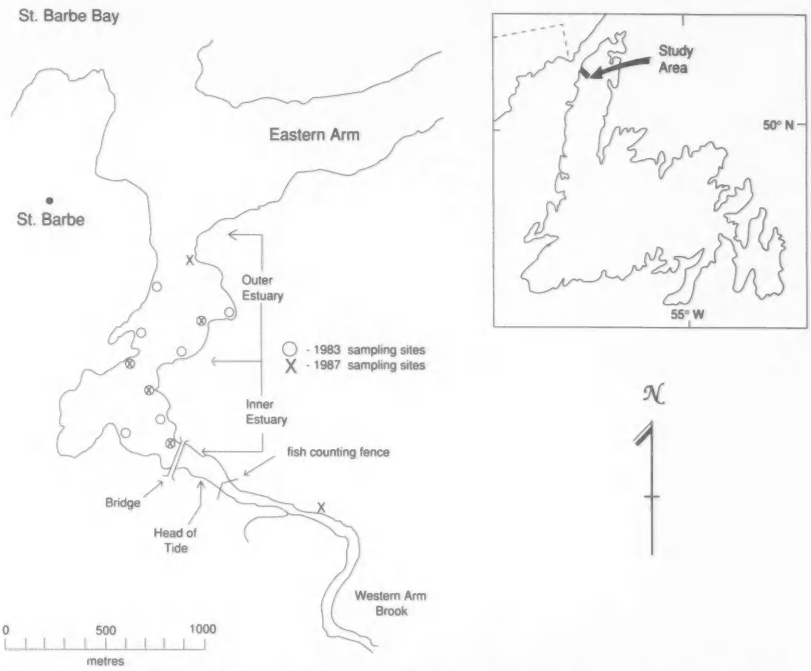

FIG. 1. Map showing location of the Western Arm Brook estuary and lower river study area.

Study Area

Western Arm Brook (Fig. 1) is a pristine, fourth-order stream in northwestern Newfoundland (51°11′N, 56°46′W) with a small drainage basin (150 km^2) that discharges into the Gulf of St. Lawrence via St. Barbe Bay. Atlantic salmon, brook trout, *Salvelinus fontinalis*, and three-spine stickleback, *Gasterosteus aculeatus*, are the most common riverine species. A complete description of the river system and its associated fauna and flora is provided by Chadwick (1982).

The estuary of Western Arm Brook (Fig. 1) is a shallow delta (total area = 65 ha) with a gently sloping bottom. Approximately 32% of the shoreline area, submerged at high tide, becomes exposed at low tide (Shears 1984). The average summer tidal fluctuation is 1.1–1.4 m. A definite channel (~5–10 m wide) bisects the estuary, especially in the upper and middle reaches. Substrate composition varies from predominantly mud-boulder-gravel at the head of the estuary and in the channel to mainly mud with extensive patches of eelgrass (*Zostera marinus*) in the littoral zones, especially in the western basin which is largely exposed at low tide. In mid-summer, a dense growth of algae (mainly *Enteromorpha* sp.) is found attached to rocks and *Zostera*. In the outer estuary, the substrate composition changes to mainly sand, gravel, and boulders with patches of *Fucus* spp. replacing the *Zostera* as the dominant vegetation along the shorelines. At low tide, water depths average 1 m in the inner estuary but 1.5 m in the outer estuary.

Daily mean water temperature in Western Arm Brook ranged from 7–12°C during the parr and smolt migration (generally mid-May to mid-June) and rarely reached 20°C in the summer. At low tide, estuarine temperature was similar to that measured in the river. The shallow nature of the estuary and frequent windy conditions precluded the establishment of a well-defined thermocline during the spring–autumn. In mid-summer, the intrusion of cooler, marine water resulted in differences in water temperature up to 6°C between high and low tide. Water salinity measurements (R. A. Cunjak, unpubl. data) indicated a poorly defined halocline but there was an increase with depth at both tidal cycles, particularly during summer when mean salinity ranged from 14–24 parts per thousand (ppt) (maximum = 30 ppt) at high tide and 7–18 ppt at low tide in the outer estuary; in the inner estuary, mean salinity ranged from 1–9 ppt and 2–14 ppt at low and high tide, respectively. In spring, when river discharge was highest, mean salinity measured 0–5 ppt (inner estuary) and 0–21 ppt (outer estuary).

Methods and Materials

All fish species captured in the fence-traps (moving upstream or downstream) were enumerated. Young salmon were classified as smolts if they had at least two of the following phenotypic characters: darkening of fins, complete body-silvering, and absence of parr marks (Wedemeyer et al. 1980); when all three of these characters were not found, fish were classified as parr. At Western Arm Brook, this distinction was always clear.

Counting-Fence Operations

The fish-counting fence located near the mouth of Western Arm Brook (Fig. 1) has been operated (May–October) since 1971. The fence consisted of aluminum conduit, spaced 16 mm apart which had a minimum efficiency of 90% in capturing smolts in Western Arm Brook (Anderson and McDonald 1978; Chadwick 1981). Because the smallest salmon parr could pass between the conduit, we considered annual totals of down-

stream migrating parr as relative rather than absolute counts (Chadwick and Leger 1986). A complete description of the fence design used at Western Arm Brook was given by Anderson and McDonald (1978).

The collection of biological characteristics of migrant salmon parr began in 1983. In that year, the counting-fence was continuously operated between May 18 (daily water temperatures <5°C) and October 24. All parr were measured (fork length, FL). From May 26 to July 4, parr were given an adipose fin-clip to identify them if subsequently recaptured in the estuary. Scales were removed from every fifth parr captured in the downstream trap until a sample of 200 was collected. In 1983, five of every 400 smolts captured in the downstream trap were sampled for FL, weight, and age determination.

In 1987, the counting-fence was operated continuously from May 12 (daily water temperatures <6°C) to October 27. All parr captured in the downstream trap were measured (FL) but the marking of individuals (fin-clips or dye injection) did not commence until May 20 after 51 parr had already passed downstream; marking ceased August 4 due to the infrequent movements of parr at the fence during summer. For the first 400 migrant parr, every tenth parr was killed and scales sampled. After the first 400 parr had moved downriver, every fifth parr was sampled. In 1987, five of every 500 smolts moving downstream were sampled.

Estuarine Studies

The distribution of salmon in the estuary was assessed both spatially and temporally by snorkeling and by sampling with a beach-seine (6-mm mesh) 30 m long and 2 m deep. Spatial distribution was determined by comparing abundance of parr or smolts at sampling sites in the estuary. Water salinity, temperature, and depth were measured at each site immediately following fish collections or dives.

In 1983, 10 sites were seined (Fig. 1) between May 28 and October 15. FL, weight, and scales were obtained from all parr captured except when $n>50$ at a site. In this case, scales were taken only from every third fish. Smolts were enumerated but not handled. The number of seine hauls made per site varied as the primary aim of the sampling was to determine the presence or absence of parr and smolts.

1987, six sites in the estuary were seined, all but one being the same as those sampled in 1983, and the effort was standardized to two seine hauls per site. Eleven collections (i.e. all sites sampled within a 24-h period) were made in the estuary between May 25 and September 15. Two further collections (September 19 and October 27) were made at three sites only in the inner estuary. FL was measured for all parr; a random collection of parr from each site was used for sex and age determination. As in 1983, smolts were enumerated but not handled.

Population estimates of parr in the estuary of Western Arm Brook were made each year using the modified Schnabel method for multiple census mark–recapture data (Ricker 1987):

$$N = \frac{\Sigma\,(c_t \cdot m_t)}{R+1},$$

where N = population size; m_t = number of parr marked from the downstream trap of the counting-fence, at the start of period t; c_t = total sample of parr captured in the estuary during period t; R = total number of recaptured parr during the year, in the estuary. Population estimates were made during four periods (May, June, July, August). Catches in the estuary after September 1 were not used because a secondary downstream movement of parr in the autumn would have confounded the estimate.

In 1983, snorkeling observations were made nine times from June 17–August 21. Each dive involved a different route in the estuary parallel to the shoreline such that all ten sites were observed from underwater at least once at both high and low tides. In 1987, snorkeling observations were made at the three sites along the eastern side of the estuary where sampling occurred in both years (Fig. 1). Observations were made at all three sites in the same day and dives were made on six different occasions from May 29–September 17. Where salmon (parr or smolts) were seen, their abundance and general behaviour (e.g. schooling, aggression) were recorded, as was water depth and description of the habitat (e.g. substrate composition, presence of a halocline). Each dive consisted of observations along four 30-m (±2 m) transects running prependicular to the shoreline at each site in the estuary.

Results

Counting-Fence Data

Although the migrations of parr and smolts were coincident, the median dates of the runs of parr (June 3, 1983 and May 31, 1987) preceded that of smolts (June 9, 1983 and June 7, 1987) by approximately 1 wk. In 1983, 1599 parr and 10 520 smolts were counted moving downstream in Western Arm Brook compared with 551 parr and 17 029 smolts in 1987. Mean water temperatures recorded during the initiation and peak of parr migrations in 1983 were 8.0 and 10.7°C, respectively; in 1987, they were 6.0 and 9.6°C, respectively.

Downstream movements essentially ceased by the end of June but a smaller, secondary movement of parr and smolts was noted in the autumn of both years (Fig. 2). In 1983, this run accounted for 140 parr and 53 smolts; in 1987, there were 78 parr and 41 smolts. Few parr were captured moving upstream through the counting-fence (Fig. 2). In 1983, there were 29 parr compared with 54 parr in 1987.

Age of parr did not differ significantly ($p=0.654$) between years, being 2.97 yr in 1983 ($n=239$) and 2.99 yr in 1987 ($n=244$). However, mean FL of downstream-migrant parr was significantly less ($p<0.001$) between years (1983: 9.9 cm, $n=1381$; 1987: 11.6 cm, $n=446$). During the downstream migrations, there was no significant correlation between capture date in the trap and FL (1983: $r=0.03$, $p>0.50$: 1987: $r=-0.11$, $p>0.05$) indicating that there was no systematic change in size with time.

Mean FL of smolts in 1983 was 16.6 cm and modal age was 4 yr (range = 3–5 yr). In 1987, smolts averaged 17.0 cm FL; modal age was 4 yr (range = 3–5 yr).

Estuary Data

The population of parr (N) residing in the estuary of Western Arm Brook in 1983 was estimated to be 14 858 with 95% confidence limits (c.l.) of 11 798 and 19 311. In 1987, N was estimated to be much less (6057 parr) with 95% c.l. of 4469 and 8271. The high estimates of N relative to the numbers of parr counted moving downstream indicate that many parr were escaping capture at the counting-fence. Assuming that the fence was installed prior to the start of the migration, only 10.8 and 9.1% of the estimated estuarine population were enumerated in 1983 and 1987, respectively.

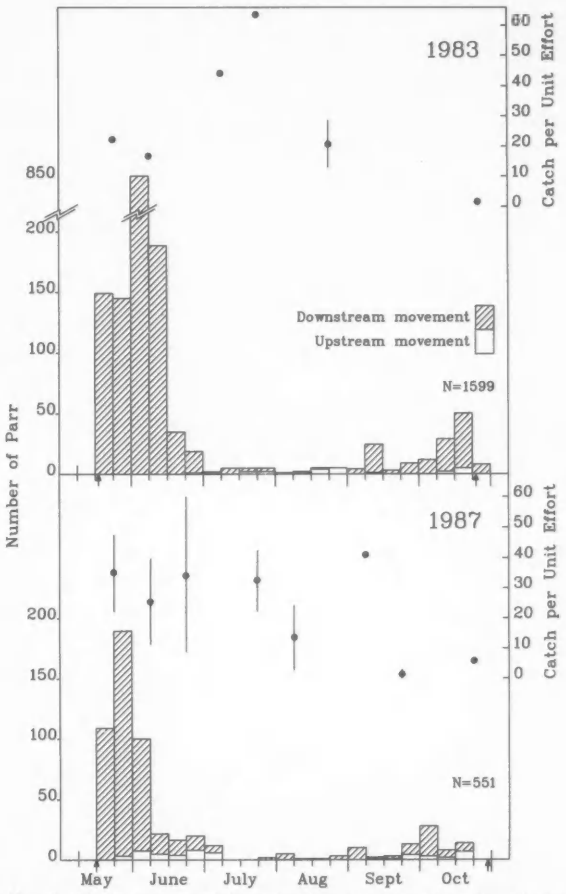

FIG. 2. Weekly counts of Atlantic salmon parr moving through the counting-fence at Western Arm Brook relative to the number of parr captured per unit effort (i.e. seine haul) at the upper site in the estuary in 1983 and 1987. CPUE points are semi-monthly means ± SD where >2 d data were collected in a period. Arrows indicate approximate dates of fence installation and removal. N = annual number of parr moving downstream through the counting-fence.

The mean FL (± SD) of salmon parr captured in the estuary of Western Arm Brook was 9.3 (± 1.56)cm in 1983, significantly less ($p<0.001$) then the mean FL of 9.9 (± 1.66)cm in 1987.

In the estuary, modal age of parr was 2 yr; age-3 parr accounted for 22% of the parr in 1983 and 35% in 1987. Parr age-4 were not found in the estuary in 1983 or in 1987. Young-of-the-year salmon were rare in the estuary; one individual was found in 1983 and in 1987.

A comparison of mean sizes of parr captured in the downsteam trap and the estuary suggested that there was some size-selection at the counting-fence. In each year, a significantly higher proportion of smaller-sized parr were captured in the estuary (Kolmogorov–Smirnov tests, $D>0.200$, $p<0.005$). In 1983, 21.1% of all parr measured during their downstream migration were <9 cm FL compared with 45.6% sampled in the estuary. In 1987, when the mean size of parr was larger, 0.9% of the parr at the fence were <9 cm FL compared with 20.7% in the estuary.

TABLE 1. Behavioural patterns and frequency of occurrence of Atlantic salmon parr and smolts in the estuary of Western Arm Brook. Data are based on underwater observations in 1983 and 1987; n = total number of salmon seen.

Site location	Life stage	n	Percent frequency: Swimming and/or aggregated	Percent frequency: Individuals holding station
Near river mouth	Parr	255	35.3	64.7
	Smolt	52	100	0
Estuary proper[a]	Parr	60	91.2	8.8
	Smolt	3	100	0

[a]Includes eight sites in estuary where parr and/or smolts observed.

Parr were most abundant at the uppermost site, near the bridge, where flows were fastest and salinities least (Shears 1984; R. A. Cunjak, unpubl. data). This site alone accounted for 63% of the parr captured in both 1983 and 1987. The snorkeling observations also indicated that salmon parr were most abundant in the inner estuary, and especially at low tide when water currents were pronounced. Parr were often holding stationary positions, on or near the bottom, and facing into the current (Table 1). Where water currents were weak such as along the margins of the estuary, at slack tides, and at most outer estuary sites, parr behaviour was similar to smolts (i.e. swimming singly or in 'loose' aggregations and occasionally in association with smolts). During high tides, parr were often found in the shallow nearshore environments which became exposed at low tide. Relatively few smolts were observed underwater (Table 1) and these were highly mobile, in aggregations, and most common during low and falling tides. There was no evidence of avoidance of salinity gradients. In both years, observations were made of parr freely moving back and forth through visible haloclines. Further, parr were seen at high tides when salinities in the immediate areas often exceeded 15 ppt, especially in the outer estuary.

The greater abundance of parr in the inner estuary was reflected in a significantly higher ($p<0.01$) catch per unit effort (CPUE) compared with the outer estuary (Table 2). The small CPUE for smolts in the estuary (Table 2) and their absence from any seine catches between late June and early September indicated that they did not reside in the estuary of Western Arm Brook for prolonged periods after downstream migration.

The CPUE data from the uppermost estuarine site (where parr were most abundant), indicated that many salmon parr remained in the estuary of Western Arm Brook throughout the summer (Fig. 2), long after the downstream migration from the river. In both 1983 and in 1987, CPUE was >10 parr per seine haul until late September–October when CPUE approached zero (Fig. 2) indicating parr had moved out of the estuary. This was evident in 1983 when few parr ($n=3$) were captured in late October in the estuary and all 10 sites were seined. Similarly, in 1987, in late September and October, seining collections yielded five and 11 parr, respectively. Parr were observed on all snorkeling dates with the exception of September 17, 1987 when, for the first time, no parr were observed underwater at any of the sites in the estuary; this corresponded to the apparent emigration of parr noted during the seining collections.

There was some evidence that the largest parr did not remain in the estuary for long. Parr >12 cm FL (considered to be the critical size for seawater adaptation, Farmer et al. 1978; Wed-

TABLE 2. Results of statistical tests to compare CPUE (expressed as the number of parr and or smolts captured per single seine haul) at sites in the inner versus outer estuary of Western Arm Brook in 1983 and 1987. Student's *t*-test was used to compare locations. *n* = the number of sample collections.

	1983			1987					
	Parr			Parr			Smolts[a]		
	n	Mean CPUE	*p*	*n*	Mean CPUE	*p*	*n*	Mean CPUE	*p*
Inner estuary	27	16.11	<0.01	32	12.23	<0.01	32	0.41	>0.10
Outer estuary	25	1.84		34	1.17		34	0.76	

[a]Smolts were enumerated in the estuary in 1987 only.

TABLE 3. Frequency of different sizes (fork length, FL) of Atlantic salmon parr marked at the counting-fence and subsequently recaptured in the estuary of Western Arm Brook, 1983 and 1987. Percent rates of recapture for each size category are given in parentheses below the frequencies.

Year	Location of mark or recapture	FL range of parr (cm) <9	9–10	10–11	11–12	>12
1983	Estuary	11	8	18	3	1
	Fence	263	363	413	157	54
		(4.2)	(2.2)	(4.4)	(1.9)	(1.9)
1987	Estuary	0	4	7	2	3
	Fence	5	24	83	109	136
		(–)[a]	(16.7)	(8.4)	(1.8)	(2.2)

[a]Not calculated due to small number of parr marked.

emeyer et al. 1980) were commonly captured at the fence, comprising 5.5 and 37.9% of the runs in 1983 and 1987, respectively. In the estuary, however, parr >12 cm FL were not found in 1983 during the period of downstream movements and only 6.7% of them were recaptured in 1987. Recapture rates of parr marked at the fence provided further evidence that large parr emigrated soon after entering the estuary, and that the size-selectivity of the counting-fence parr was similar between years. In both years, the recapture rate in the estuary of parr marked at the fence was <5% (1983; 3.3%, 1987; 4.4%). Large parr were recaptured with least frequency (Table 3). Smaller parr generally had higher recapture rates (Table 3) suggesting that their residence in the estuary was longer than that of large parr.

Discussion

The results clearly establish that juvenile Atlantic salmon in Western Arm Brook use the estuary as a temporary rearing environment after migrating downstream. Further, the estimated population size of parr inhabiting the estuary indicate that their numbers represent a significant proportion of the river's total production of salmon. Although the annual estimates of *N* varied considerably, the yearly totals of migrant salmon (i.e. *N* + smolts) were similar for both years (1983; 25 378 migrants, 1987; 23 086 migrants).

The utilization of estuarine environments by juvenile Atlantic salmon is not unique to Western Arm Brook. Randall and Power (1979) and Power et al. (1987) reported on the growth and movements of juvenile salmon (postsmolts) in estuaries along the Quebec North Shore and the Ungava coast, respectively. The habitation of estuaries by Atlantic salmon parr has also been documented, but studies have generally been of a preliminary or descriptive nature. Huntsman (1945) noted their presence in the estuary of the Margaree River in Nova Scotia but dismissed the occurrence as being the result of displacement from upstream. Power and Shooner (1966) sampled parr from a single location in the Nabisipi River estuary (Quebec) during one summer and found that parr were predominantly age-3 females which grew well in this environment. The present study provides information on the population characteristics, distribution, and general behaviour of Atlantic salmon parr sampled throughout an estuary during 2 yr of study (May–October) in relation to smolts and parr migrating downstream.

Although the estuarine population of salmon parr in Western Arm Brook is considered to be derived from migrants originating upstream, there were notable differences in the size and age composition of parr sampled at the counting-fence and in the estuary. A number of explanations can account for these discrepencies. As noted earlier, we consider the counting-fence to be size-selective. The problem was most pronounced in 1983 when mean sizes of parr were smaller allowing more to escape capture. Such selectivity at the fence would account for the lower modal age in the estuarine population of parr, the relatively greater abundance of parr in the estuary, and the low percentage of parr (<5%) initially marked at the fence and recaptured in the estuary.

The few parr which may have entered the estuary prior to fence installation and/or after fence removal the previous autumn was insufficient to account for the discrepencies in the migrant and estuarine population characteristics. The first sampling of the estuary in 1987 was made on May 24 at two sites in the inner estuary, but yielded only five parr. This was the lowest CPUE found at these sites until late October, following fence removal, when a similarly low CPUE of 3.0 was found. Recent collections at these same sites on May 19, 1988 (R. A. Cunjak, unpubl. data) prior to fence installation (water temperature = 4.0°C) yielded no salmon parr. These data support our view that parr begin entering the estuary of Western Arm Brook during the spring as minimum water temperatures exceed 4°C and that few parr remain to overwinter.

The relatively few large parr (i.e. >12 cm FL) captured in the estuary may represent an emigration seaward by these parr after the attainment of a critical size for smoltification (Parry 1960; Farmer et al. 1978; Wedemeyer et al. 1980; Healey 1982) since there was little upstream movement by parr in Western

Arm Brook (1983; $n = 31$, 1987; $n = 62$). Smaller parr may be precluded from an immediate entry to the sea until they are physiologically adapted to a saline environment (Huntsman and Hoar 1939; Parry 1960; Hoar 1976). The variable salinities (temporal and spatial scale) of estuaries provide an ideal transition environment for such a process, as suggested by other researchers (Power and Shooner 1966; Iwata 1981; Healey 1982).

It seems likely that many of those parr not completing smoltification in the estuary return upriver to overwinter. In support, recent data (R. A. Cunjak, unpubl. data) have shown that some parr marked in 1987 had returned to the estuary the following spring as parr ($n = 15$) or as smolts ($n = 4$). It should be noted that the smolt estimate is a minimal one since so few were handled and examined for marks. That few parr were enumerated moving upstream to account for the overwintering migration may be explained by the relative difficulty in capturing fish while moving upstream through a counting-fence (e.g. Symons 1969). Saunders and Allen (1967) estimated that only 51% of smolts moving downstream were captured by a fence on the Miramichi River, N.B. The proportion of parr escaping capture during their upstream migration in Western Arm Brook is unknown at present, but we believe that because of their small size and the direction of movement, the proportion is at least 50% and likely much greater.

The downstream migration of parr and smolts in the autumn (September–October) of 1983 and 1987 at Western Arm Brook was also noted in previous years (E. M. P. Chadwick, unpubl. data). Power (1969); Riddell and Leggett (1981); Youngson et al. (1983); and Hutchings (1985) have also noted autumnal downstream migrations of Atlantic salmon parr. However, only the study of Hutchings (1985) found that these migrants continued their movement into brackish water. In the estuary of Western Arm Brook, a corresponding increase in parr abundance was found in the estuary in the autumn (late September). Most of the parr were notably 'silver' and when these same sites were sampled (and snorkeled) a week later, parr were almost entirely absent. We inferred from this a final seaward movement. The possibility of an autumnal smoltification may be related to the occurrence of environmental 'threshold' levels of water temperature and/or daylength (see McCormick et al. 1987) similar to those encountered during the spring migration.

The population of salmon parr inhabiting the estuary of Western Arm Brook is dynamic and not evenly distributed, being more abundant in the inner estuary. Unlike smolts which have a short residence time in the estuary, parr were found from May to October but were most numerous coincident with, and just following, downstream migrations from the river. We hypothesize that many of the largest parr emigrate seaward as a consequence of the completion of smoltification, the remainder return upriver to overwinter.

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Some Properties of a Finite Cell Line from Beluga Whale (*Delphinapterus leucas*)[1]

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A finite cell line (BWK) was derived from kidney of an immature male beluga whale (*Delphinapterus leucas*). Cells were grown for 19 ± 1 passages at 37°C in enriched tissue culture media supplemented with 10% fetal bovine serum and containing antibiotics. The cell line had a diploid chromosome modal number (2n = 44), but a pseudodiploid karyotype. BWK cells were characterized by lactate dehydrogenase (LDH), malate dehydrogenase (MDH), glucosephosphate isomerase (GPI), and phosphoglucomutase (PGM) isozyme systems. The cells were susceptible to infection by several mammalian viruses including coxsackievirus (B3 and B5), vaccinia, and herpes simplex 1; but were refractory to echovirus 27, influenza A, poliovirus (types 1 and 3), and simian agent 11. The BWK line, which has been stored in liquid nitrogen, appears to be suitable for isolation of viruses from marine mammals.

Une lignée cellulaire finie (BWK) a été tirée du rein d'un béluga mâle immature (*Delphinapterus leucas*). Les cellules ont été cultivées par 19 ± 1 passages à 37°C dans un milieu de culture de tissus enrichi avec 10% de sérum de foetus de bovin et contenant des antibiotiques. La lignée cellulaire possédait un nombre modal de chromosomes de type diploïde (2*n* = 44) mais un caryotype pseudodiploïde. Les cellules BWK se caractérisaient par des systèmes d'isozymes de la lactate-déshydrogénase (LDH), de la malate-déhydrogénase (MDH), de la glucose phosphate isomérase (GPI) et de la phosphoglucomutase (PGM). Les cellules étaient vulnérables à l'infection par plusieurs virus mammaliens, notamment le virus Coxsackie (B3 et B5), la vaccine et l'herpes simplex 1, mais étaient réfractaires à l'échovirus 27, au virus A de la grippe, au poliovirus (types 1 et 3) et à l'agent simien 11. La lignée BWK, qui est gardée dans l'azote liquide, semble convenir à l'isolement des virus chez les mammifères marins.

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Many terrestrial mammalian cell lines are available in tissue culture. These cell lines have proven to be invaluable for research progress in cellular physiology, in vitro toxicology, and diagnostic virology. Presently there are only two continuous marine mammal cell lines. The first is a kidney cell line (Sp 1 K) established from the Atlantic spotted dolphin (*Stenella plagiodon*) by Pirtle and Kniazeff (1968) and now available from the American Type Culture Collection (ATCC) Cell Respository (Hay et al. 1983). The second is a sea lion dermal cell line established from a biopsy of focal dermatitis (Smith 1982, as cited by Britt and Howard 1983).

Noncontinuous cell lines have been derived from tissues from several marine cetacean species including the fin whale, *Balaenoptera physalus* (Kniazeff and Groyon 1966); shortfin pilot whale, *Globicephala macrorhynchus*, common dolphin, *Delphinus bairdi* (now *D. delphis*) and bottlenose dolphin, *Tursiops gilli* (now *T. truncatus*) (Pirtle and Kniazeff 1968); gray whale, *Eschrichtius robustus* (Arnason 1981; Mathews et al. 1988) narwhal, *Monodon monoceros* (Andrews et al. 1973); bowhead whale, *Balaena mysticetus* (Smith et al. 1987); Pacific whiteside dolphin, *Lagenorhynchus obliquidens* (Cecil and Nigrelli 1970a); and beluga whale, *Delphinapterus leucas*) Jarrell and Arnason 1981).

Many of the above cell lines were specifically derived for short-term karyological or virological studies and were propagated only briefly in the laboratory. Thus, further tissue culture applications have obviously been hampered by the general lack of availability of characterized cetacean cell lines (both continuous and noncontinuous). In the present study we describe the karyology, isozyme expression, cellular growth characteristics, and viral susceptibility of a finite cell line that was derived from kidney tissue of beluga whale (Nielsen et al. 1986). The present report establishes criteria for standardization of cetacean cell lines and further demonstrates the feasibility of using such cryopreserved cetacean cells from early passage level cultures as defined systems for subsequent diagnostic virology and comparative biochemistry.

Materials and Methods

Media

A previous report from the ATCC suggested that enriched tissue culture media was required for optimal growth of the

[1]A portion of these results was presented at the 37th Annual Meeting of the Tissue Culture Association, Chicago, IL., June 4–8, 1986.

dolphin kidney (Sp 1 K) cell line (Hay et al. 1983). Therefore, we elected to use either of the following enriched, modified tissue culture media for culturing beluga whale kidney (BWK) cells:

(A) Growth medium 1 (GM1) consisted of Eagle's basal medium (EBM) with Earle's salts, enriched with double-strength nutrients (i.e. amino acids, 2×; vitamins, 2×; L-glutamine, 2×) and supplemented with 10% fetal bovine serum (FBS). (All ingredients were from GIBCO Laboratories, Life Tech., Inc., Grand Island, NY.)

(B) Growth medium 2 (GM2) consisted of Eagle's modified minimum essential medium (MEM), with Hanks' balanced salt solution which was supplemented (per 100 mL) with 2 mL of 200 mM L-glutamine (GIBCO); 10 mL of FBS; 2 mL of (100×) amino acids for EBM (Flow Laboratories, McLean, VA); and 2 mL of (100×) vitamins for EBM (Flow Labs).

Each medium was buffered with sterile $NaHCO_3$ solution and adjusted to pH 7.0–7.2 prior to use. Cells were propagated in either of the above media (i.e. GM1 or GM2) with added antibiotics, as subsequently specified.

Cell Culture Initiation and Maintenance

Primary cell cultures were initiated from a kidney of an immature (3.30 m, 540 kg) male beluga whale (Nielsen et al. 1986). Cells were enzymatically dissociated from the minced kidney tissue by modification of the method of Montes de Oca (1973) as previously described (Nielsen et al. 1986). The tissue was diced into small (2–3 mm^3) pieces, rinsed several times in phosphate buffered saline (PBS) without Ca^{2+} or Mg^{2+} and dispersed with a magnetic stirrer at room temperature in PBS containing 0.1% collagenase, 0.25% trypsin, 0.02% disodium ethylenediamine tetraacetic acid (EDTA), and 0.012% methylcellulose. Harvested cells were decanted. The cell suspensions were filtered through several layers of sterile gauze, collected by centrifugation (183 × *g*, 20 min), washed in medium and resuspended in GM1 supplemented with antibiotics (each millilitre contained 200 IU of penicillin, 200 μg of streptomycin and 250 μg of gentamicin sulfate). Cells were seeded into replicate 75-cm^2 plastic flasks (Corning Corp., Corning, NY). Greater than 90% of the beluga cells were viable at the time of cell culture initiation, as determined by the trypan blue exclusion method of Hoskins et al. (1956). Cell cultures were incubated at 37°C. After 24 h, medium was replenished. Medium was subsequently replenished weekly (or whenever the pH became acidic) until monolayers eventually became confluent (about 4 wk).

Thereafter, cells were routinely maintained by application of standard tissue culture procedure (Merchant et al. 1964). Thus, BWK cells were readily grown at 37°C as monolayer cultures in GM1 supplemented with 100 IU·mL^{-1} of penicillin and 100 μg·mL^{-1} of streptomycin, or in GM2 with 50 μg·mL^{-1} gentamicin sulphate added. The BWK cells were generally subcultured every 2 to 3 wk at a 1:2 split ratio by dispersal with 0.01% trypsin–0.02% EDTA (Merchant et al. 1964). Supplementary stocks of early passage level BWK cells were preserved frozen in enriched medium with 10% dimethyl sulphoxide in ampules in liquid nitrogen (Shannon and Macy 1973).

For photomicroscopy, cell cultures that were grown on coverslips were fixed in absolute methanol and stained with May-Grunwald-Giemsa stain in the manner described by Merchant et al. (1964).

Mycoplasma

The BWK cells were tested for the presence of mycoplasma and bacteria by using the direct culture method (Mycotrim-TC, Hana Media Inc., Berkeley, CA). No evidence of growth by these two contaminants was noted.

Karyology

Culture flasks containing 70% confluent, actively growing, BWK cells were exposed to medium containing colcemid (0.05 μg·mL^{-1}) for 6 h. Cells were harvested, fixed, and chromosome spreads were prepared for counting according to the method of Earley (1975). Solid-stained preparations were made by staining slides in dilute Giemsa for 6 min. The chromosome modal number was determined for 50 cells at passage level 7 and again at passage level 14. The sequentially C-banded karyotype was determined in detail for cells at passage level nine. The C-bands were visualized according to the method of Sumner (1972). The BWK cell karyotype was arranged by using the previously published model for beluga whale by Jarrell and Arnason (1981).

Isozyme Electrophoresis

Enzymes were extracted from actively growing BWK cell cultures, BWK cells frozen in ampules, and from ampules (obtained from the ATCC; CCL No. 78) of the Sp 1 K (NBL-10) cell line from spotted dolphin by the freeze–thaw procedure of Shannon and Macy (1973). The procedure was modified by increasing the cell concentration 10-fold prior to extraction, and the final medium contained 0.3 mg·mL^{-1} of both nicotinamide adenine dinucleotide (NAD) and nicotinamide adenine dinucleotide phosphate (NADP). After centrifugation (20 000 × *g*, 30 min) a single crystal of sucrose was added to each (~0.1 mL) sample.

Enzymes were extracted from beluga whale kidney tissue by homogenization in a Teflon and glass tissue grinder with an equal volume of 0.25 M sucrose solution. Extracts to be used for electrophoresis of glucosephosphate isomerase (GPI) and phosphoglucomutase (PGM) also contained 0.3 mg·mL^{-1} NADP, while extracts to be used for electrophoresis of lactate dehydrogenase (LDH) and malate dehydrogenase (MDH) contained 0.3 mg·mL^{-1} NAD. Homogenates were clarified by centrifugation at 40 000 × *g* for 20 min. The supernatant was diluted 1:10 with sucrose/NAD or NADP solution, prior to electrophoresis.

Starch gel electrophoresis of the cell culture and tissue extracts was carried out using the semimicro technique of Tsuyuki et al. (1966). The electrophoresis buffer system for separation of all isozymes (LDH, MDH, GPI, and PGM) was N-(3-aminopropyl)-morpholine/citric acid pH 6.1 (Clayton and Tretiak 1972). LDH and MDH isozymes were visualized as described previously (Clayton and Gee 1969; Clayton et al. 1971). GPI isozymes were stained in a 0.1 M Tris (pH 8.0 HCL) solution containing 1 mg·mL^{-1} of $MgCl_2 \cdot 6H_2O$, 1.5 mg·mL^{-1} of fructose-6-phosphate, 2 units·mL^{-1} of glucose-6-phosphate dehydrogenase, 0.2 mg·mL^{-1} of NADP, 0.2 mg·mL^{-1} of nitroblue tetrazolium (NBT), and 0.02 mg·mL^{-1} of phenazine methosulphate (PMS). PGM isozymes were stained in a 0.15 M Tricine solution (pH 8.0 NaOH) that also contained 2.5 mg ($MgCl_2 \cdot 6H_2O$)·mL^{-1}, 5 mg(glucose-1-phosphate)·mL^{-1}, 2 units (glucose-6-phosphate dehydrogenase)·mL^{-1}, 0.5 mg (NADP)·mL^{-1}, 0.5 mg (NBT)·mL^{-1} and 0.03 mg (PMS)·mL^{-1}.

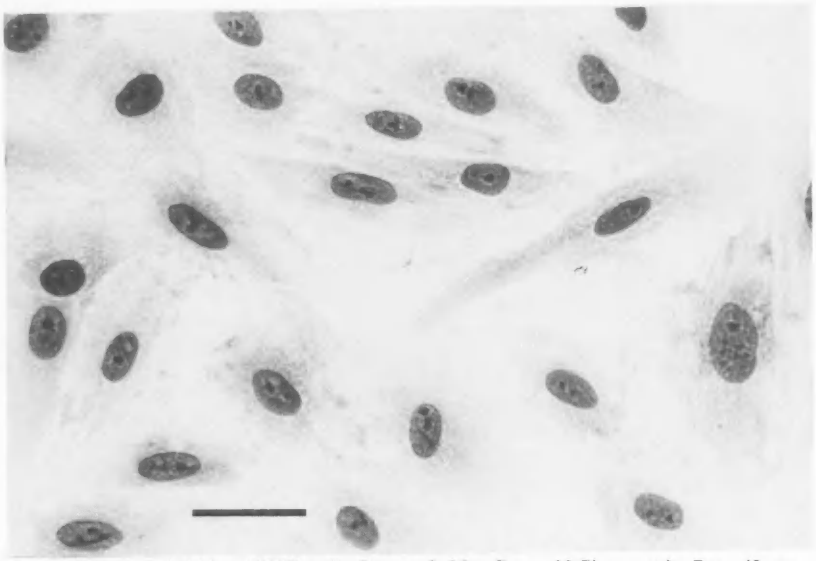

FIG. 1. Beluga whale kidney (BWK) cells. Passage 9. May-Grunwald-Giemsa stain. Bar = 40 μm.

Viral Susceptibility

The following representative array of mammalian viruses was used to determine the viral susceptibility of BWK cells: Poliovirus (types 1 and 3), echovirus (27), coxsackievirus (B3 and B5), herpes simplex virus 1, vaccinia virus, influenza virus (A PR8), and simian agent (SA11) which is a rotavirus. The picornaviruses were propagated in Buffalo green monkey kidney cells (BGMK). When generalized cytopathic effects (CPE) were evident, the infected cell cultures were frozen–thawed (3×) to release cell-bound virus, and the virus-containing fluids were semi-purified by differential centrifugation followed by filtration through 0.45-μm pore diameter filters. The SA11 was grown in simian (MA-104) cells and similarly processed, but not filtered before use. The herpesvirus was grown in BGMK cells; whereas the vaccinia virus was propagated in human (HeLa) cells and the influenza virus in L cells. The latter three viruses were used as crude virus stocks, preclarified by slow speed centrifugation at 4°C to remove cellular debris.

For infectivity assays confluent monolayers of BWK cells (passage levels 15–17) in 25-cm^2 flasks were used. Cells in GM2 containing 50 $\mu g \cdot mL^{-1}$ of gentamicin sulfate were propagated at 37°C in an atmosphere containing approximately 1% CO_2. The media were removed from the cell cultures and the monolayers were inoculated with 0.25 mL of a virus or with 0.25 mL of GKN (diluent control, consisting of 0.1% glucose, 0.04% KCl, and 0.8% NaCl). After adsorption for 1 h, 5 mL of GM2 was added to each flask as a liquid overlay. The infected cells were incubated at 37°C in a CO_2 incubator for at least 10 d and observed daily for CPE. If any cytopathology was observed, BWK cells were considered presumptively susceptible and the cultures were frozen. Later, 0.25 mL of fluid from each of the frozen cultures both undiluted and diluted 1:100 was used to inoculate additional monolayers of BWK cells. Cells were reincubated at 37°C and observed daily for CPE. The appearance of CPE indicated that the virus infection was passaged to another set of BWK cells, and BWK cells were considered to be susceptible to virus infection and multiplication.

Results

The BWK cell cultures contained both epithelioid and fibroblastic cell types with the latter apparently predominating (See Fig. 1). Mature cultures, which grew readily at 37°C in either GM1 or GM2, appeared as contact-inhibited cell monolayers that could be transferred (or passaged) by standard tissue culture procedures (Merchant et al. 1964). Cells became increasingly granular, however, beyond passage level 17. By passage level 19 ± 1 cell growth had reached a plateau and cultures could no longer be propagated in the usual manner. With periodic replenishment of media, these cultures were maintained in the Winnipeg laboratory in a steady-state condition for over a year without transfer. Significantly, cell cultures that had been revived in Honolulu from frozen ampules of early passage BWK stock exhibited a similar finite life span (i.e. cells could not be serially propagated beyond passage 20).

The BWK cell line exhibited a diploid mode (2n = 44) when chromosomes were counted at passage levels 7 and 14. In a detailed karyotype for cells at passage level 9 (Fig. 2) chromosomes appeared normal with no evidence of chromosomal aberrations or overt rearrangements, but the distribution of constitutive heterochromatin within some homologous pairs differed very slightly from the published karyotype for this species (Jarrell and Arnason 1981).

Zymograms of Fig. 3 show that GPI (Fig. 3c) and PGM-1 (Fig. 3d) isozymes clearly distinguish BWK and Sp 1 K cells while the mobilities of MDH (Fig. 3a) and LDH (Fig. 3b) isozymes are the same in both cell lines. In all isozyme systems the mobilities of the isozymes from BWK cells and from beluga whale kidney tissue are identical. Although only one electrophoresis condition (buffer composition, pH etc.) is represented in Fig. 3 for each isozyme system, more were tested, and in contrast to the situation with GPI and PGM-1 no set of conditions was found that would reveal different mobilities for BWK and Sp 1 K MDH or LDH.

The BWK cells at passages 15–17 were susceptible to coxsackievirus (B3 and B5), vaccinia, and herpes simplex 1;

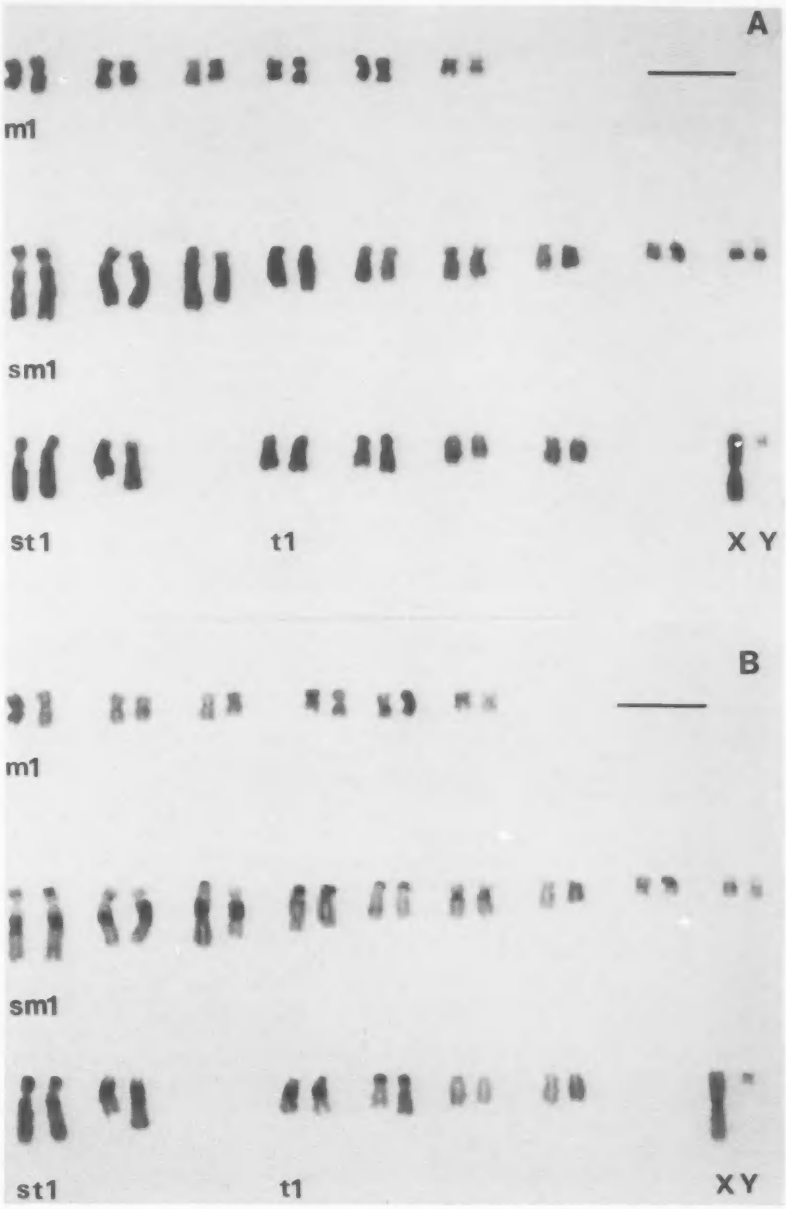

FIG. 2. Beluga whale cell chromosomes (2n = 44). Bar = 10 μm. (A) Solid-stained karyotype of BWK cells (passage level 9). (B) Sequentially C-banded karyotype.

but were refractory to echovirus (27), influenza A (PR8), poliovirus (types 1 and 3) and simian agent (SA11). No attempts were made to adapt the culture-negative viruses to BWK cells by serial blind passage of virus beyond passage 2, in the manner used by Cabasso et al. (1957) for adapting infectious bovine rhinotracheitis virus to HeLa cells.

Discussion

Fibroblastic cell cultures derived from normal tissues of terrestrial vertebrates usually have a limited or finite proliferative capacity. This phenomenon has been most extensively studied in the case of human diploid fibroblasts which generally cannot undergo more than about 50 population doublings in cell culture (Hayflick 1965; 1968). This aging of cell populations in vitro has been correlated by many investigators with senescence of the whole organism (Macieira-Coelho 1988). Although the in vitro proliferative capacity of cells from a given tissue is both species specific and reproducible, there is presently insufficient data to make accurate interspecies comparisons relating population doublings of cells in culture to the natural lifespan of the donor animal (Cristofalo et al. 1977).

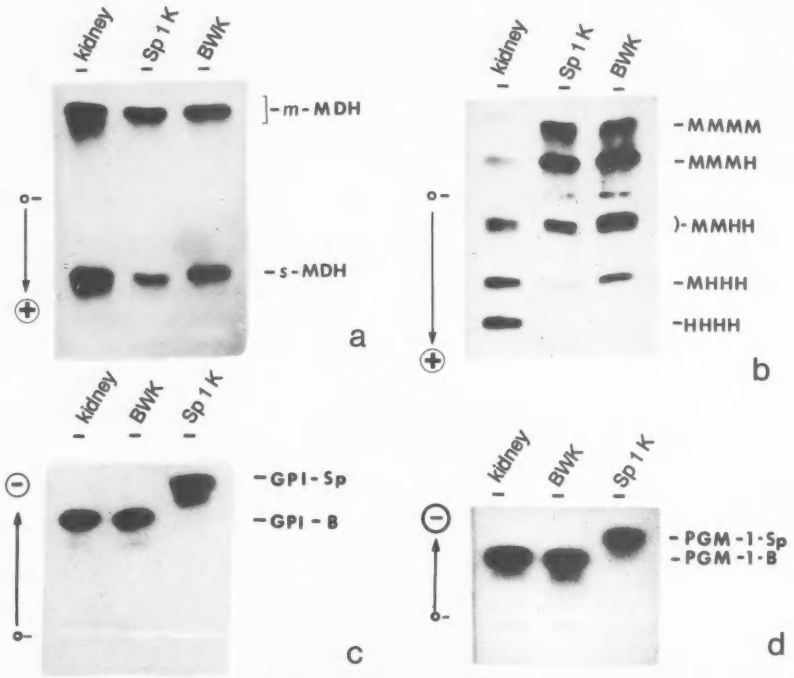

FIG. 3. Zymograms of beluga whale tissue and cultured cell enzymes (starch gel electrophoresis at pH 6.1). (a) Malate dehydrogenase (MDH), (b) Lactate dehydrogenase (LDH), (c) Glucosephosphate isomerase (GPI), (d) Phosphoglucomutase (PGM), kidney = extract of beluga whale kidney, Sp 1 K = spotted dolphin culture cell extract, BWK = beluga whale cultured cell extract.

The beluga BWK cell cultures demonstrated a similar finite lifespan, or proliferative capacity, in both the Winnipeg and Honolulu laboratories. Whether this represented the natural phenomenon of senescence in vitro referred to previously, or was an undiscovered nutritional deficiency problem, is unclear. Attempts by Andrews et al. (1973) to grow narwhal cells in MEM with 20% FBS resulted in cultures which were initially successful, but which ceased to thrive after several cell passages. Similar results were obtained by Smith et al. (1987) who reported that bowhead whale cells grew slowly in vitro, and cultures could not be propagated beyond six to nine passages. These two reports both seem to support the finite lifespan hypothesis. Certainly, cetacean cells are comparatively difficult to culture, as evidenced by comments in the ATCC catalogue relating to the culture of Sp 1 K cells in nonenriched medium (Hay et al. 1983).

There is a general conservatism of chromosomal evolution in cetaceans (Arnason 1972). Therefore, comparisons of karyotypes of monodontid and delphinid cetaceans have focussed on variations in C-heterochromatin rather than on overt differences in chromosome morphology (Jarrell and Arnason 1981, Arnason 1980). Intrapopulational differences in C-heterochromatin distribution have not been extensively studied. In the present study early passage level BWK cultures were not sacrificed for karyological analyses; instead, efforts were devoted toward obtaining maximum numbers of cells in culture. Although the karyotype of BWK cells at passage level 9 (Fig. 2) appeared similar to that for *Delphinapterus leucas* published by Jarrell and Arnason (1981), certain minor changes have likely occurred in the cell cultures with increased cell passage, as evidenced by our further observation of minor variations in C-banding patterns between individual BWK cells. Therefore, the finite BWK cell line can best be described as pseudodiploid, rather than diploid, as based upon evidence derived from the sequentially C-banded karyotype (Fig. 2B). Unfortunately, insufficient dividing cells were present in the apparently senescent BWK cultures at passage levels 18–20 to allow us to document changes occurring later in the terminal cultures.

Isozyme electrophoresis is a convenient and extensively used means of identifying cell lines (O'Brien et al. 1980). We have not sought to provide a definitive set of isozymes that will distinguish BWK cells from all other cell lines but it is clear (Fig. 3) that GPI and PGM-1 are sufficient to distinguish BWK and Sp 1 K cells while the electrophoretic mobilities of MDH and LDH isozymes are evidently the same in both of these related species. As well, the same electrophoretic mobilities in extracts from beluga whale kidney and BWK cells for all the isozyme systems provides a measure of confidence in their identity.

The variety of viruses which infect marine mammals has not yet been determined. Many unexplained mortalities have occurred in whales and dolphins both in captivity and in the wild that may have had a contributing viral etiology (Britt and Howard 1983). To date, diagnostic virology of cetaceans has relied heavily on application of standard veterinary procedures with the supplemental use of cell lines from terrestrial mammals. This is due in large part to the obvious lack of adequately characterized cetacean cell lines. Apparently only the Sp 1 K line has been tested against a broad array of viruses, and this test series did not include echoviruses, rotaviruses, or caliciviruses. Thus, the Sp 1 K cell line was reported to be suscep-

tible to coxsackievirus (A9 and B5), herpes simplex, vaccinia, influenza A, parainfluenza 3, reovirus 3, adenovirus 5, vesicular stomatitus virus, infectious bovine rhinotracheitis virus, bovine viral diarrhea agent, hog cholera virus, and a variety of encephalitus viruses (Hay et al. 1983; Kniazeff and Groyon 1966). The Sp 1 K cells were refractory only to poliovirus 2 (Hay et al. 1983). In contrast the fibroblast-like cell lines from the Pacific whiteside dolphin were susceptible to coxsackievirus types A9, B3, B4, but not to coxsackievirus types B1, B2, B5, B6 (Cecil and Nigrelli 1970b). These cells were also susceptible to reovirus (1 and 3) but not adenovirus 12. Other viruses were not tested, so detailed comparisons with the BWK line are not feasible. The stock cultures of BWK cells in ampules will undoubtedly be useful for additional studies in diagnostic virology.

Acknowledgments

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Responses of Cod (*Gadus morhua*) and Haddock (*Melanogrammus aeglefinus*) to Baited Hooks in the Natural Environment

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Løkkeborg, S., Å. Bjordal, and A. Fernö. 1989. Responses of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) to baited hooks in the natural environment. Can. J. Fish. Aquat. Sci. 46: 1478–1483.

The behaviour of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) towards baited hooks was observed in the sea with underwater television. Both species exhibited a diel rhythm of feeding activity, most pronounced in cod, with an increase at dawn and a decrease at dusk. The activity rhythm of cod changed from bimodal with peaks in the morning and afternoon in September, to unimodal in December. Haddock showed a less clear activity rhythm during daytime. Activity of fish decreased at high current velocities. Both cod and haddock swam upstream towards baited hooks. More haddock responded to the bait than cod, but haddock showed a less intense response characterized by biting repeatedly at parts of the bait, whereas cod completely ingested the bait and thereby increased the probability of getting hooked. The observed difference in hooking behaviour between cod and haddock explains differences between the species found in longline fishing trials with different bait sizes and hook designs.

Le comportement de la morue (*Gadus morhua*) et de l'aiglefin (*Melanogrammus aeglefinus*) devant des hameçons appâtés a été observé en mer à l'aide de caméras de télévision sous-marines. Les deux espèces affichent un rythme diel d'activité alimentaire, plus prononcé chez la morue, avec une augmentation à l'aube et une diminution au crépuscule. Le rythme d'activité de la morue passait d'un rythme bimodal avec des pointes le matin et l'après-midi en septembre, à un rythme unimodal en décembre. L'aiglefin affichait un rythme d'activité moins bien défini pendant la journée. L'activité du poisson diminuait en présence de forts courants. La morue et l'aiglefin s'approchent tous deux des hameçons appâtés à partir de l'amont. Un plus grand nombre d'aiglefins que de morues ont été trompés par l'appât, mais la présence de l'aiglefin était moins forte, caractérisée par des morsures répétées à certaines parties de l'appât, tandis que la morue ingérait complètement l'appât, ce qui augmentait la probabilité de capture. La différence observée dans le comportement à l'accrochage des morues et des aiglefins explique la différence que l'on relève entre les espèces dans les essais de pêche à la palangre avec des appâts de tailles différentes et des types d'hameçons différents.

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Longlining is a traditional fishing method in many regions (Bjordal 1981; von Brandt 1984). When trying to improve the efficiency of the gear, knowledge about the behaviour of the fish towards the baited hooks is essential (Fernö et al. 1986).

Field studies on the behaviour of fish towards fishing gear have advantages over both laboratory experiments and comparative fishing trials (Løkkeborg 1985). In the laboratory, fish may be conditioned to selected food odours (Pawson 1977; Solemdal and Tilseth 1984) or influenced by the artificial environment, whereas fishing trials give no information about the cause of an observed difference. However, few field studies on fish behaviour in relation to longlines have been made (but see Johnstone and Hawkins 1981; Fernö et al. 1986), and none gives a general description of how commercially important species behave towards baited hooks.

Systematic observations of fish in the open sea are difficult to make from a vessel. The present study was therefore conducted from an oil platform, which has proved to be ideal, providing stable concentrations of fish at a weather-independent observation site (Bjordal and Fernö 1983).

Cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) are two important target species in the Norwegian longline fishery (Løkkeborg 1987). Fishing trials with several bait sizes and hook designs have demonstrated a difference in catchability between these species (Johannessen 1983; Skeide et al. 1986). An objective of the present field study was to explain this difference by studying the behaviour of cod and haddock towards baited hooks. In addition, diel activity rhythms and the influence of current velocity and direction were investigated.

Materials and Methods

The observations were carried out from the oil platform Albuskjell 1/6 A at the Ekofisk field in the North Sea (56°38′34″N, 02°56′24″E) during two periods, from December 1 to 9, 1983, and from September 8 to 16, 1984.

A light-sensitive underwater television camera (Hydro Products TC-125 SIT-W) was mounted horizontally in an aluminium

frame (see Sutterlin et al. 1982). A 2.7-m long test line was attached to two poles on the frame and positioned 1.5 m from the camera and 0.5 m above the bottom. Four hooks (Mustad Norway, Qual. 7269, No. 5) with 25-cm long snoods were attached to the test line 45 cm apart. To enable observations during the night, a 500-W lamp with a red filter (Kodak Wratten No. 29) was used and set at 60% power both day and night. The visible distance was taken to be 3–4 m and was nearly constant during the 24-h cycle.

The baits used were pieces of mackerel (*Scomber scombrus*; 2 cm wide and 4–5 cm long) and two different artificial baits, but two of the four hooks were always baited with mackerel, and a majority of the biting responses and hookings were made on the mackerel bait (75 and 77%, respectively). This paper therefore exclusively describes fish behaviour towards mackerel bait.

The current speed and direction were recorded every 12 min during the period in September by a current meter (SD-1000, Sensordata A/S; accuracy: 0.1 cm/sec) suspended 3 m above the bottom.

Observations were made both day and night. At the beginning of each trial, the test line was baited with mackerel and one of the artificial baits on alternating hooks, and the frame placed on the bottom at a 70-m depth. Each trial lasted for 3 h or until there were free baits of only one type left. The baits were replaced before each new trial and their relative positions changed. During the December and September period, there were 27 and 58 trials, respectively.

All fish observations were videotaped for later analysis. Time of appearance of each fish and its species were recorded. The swimming direction relative to the current was recorded as down-current, up-current, or across-current for fish with approximately straight swimming directions in periods where the current direction could be determined by the plankton drift.

A fish would often leave and re-enter the field of view. If the fish was out of view for more than 1 min, the next arrival was recorded as a new fish. If several fish of the same species and size simultaneously left and entered the field of view, all arrivals were recorded as new fish.

When investigating the diel activity rhythm and the influence of current velocity and direction, the fish were categorized as:

Not responding; fish swimming by without apparent reaction to the baits,

responding; fish responding to a bait, regardless of type, by showing any of the behaviour patterns defined below.

The following behaviour patterns were used to categorize the behaviour of fish responding to the mackerel-baited hooks:

Approach; swimming towards the bait and turning without touching the bait,

taste; touching the bait with the lips or the barbel (if tasting was followed by another behaviour pattern, the taste had to last for at least 1 s to be recorded),

incomplete bite; biting the bait while a part of it was outside the mouth or sucking the bait into the mouth without closing the mouth,

complete bite; sucking the whole bait into the mouth and closing the mouth,

bite; either an incomplete or a complete bite,

chew; chewing on the bait,

pull; swimming slowly with the bait in the mouth,

jerk; a rapid movement of the head with the bait in the mouth,

shake; at least four rapid jerks following each other,

rush; swimming rapidly forward with the bait in the mouth,

bait out of mouth; spitting the bait out of the mouth or having the bait pulled out,

hooking; retaining the hook in the mouth for at least 20 s after a jerk or a rush while the fish fights violently,

behaviour sequence; a series of behaviour patterns made towards the same bait. The sequence terminated when the fish turned away from the bait.

TABLE 1. Number of observed cod and haddock in the two observation periods.

Species	Period	No. of observed fish	Observation time (h)
Cod	Dec. 1983	840	79.3
	Sept. 1984	2116	123.3
Haddock	Dec. 1983	209	79.3
	Sept. 1984	651	123.3

Results

Cod and haddock were the most abundant fish in the area. Other species observed were saithe (*Pollachius virens*), ling (*Molva molva*), Atlantic catfish (*Anarhichas lupus*) and plaice (*Pleuronectes platessa*). A total of 2956 cod and 860 haddock were recorded (Table 1). The mean length of fish that were caught on the mackerel-baited hooks was 56.7 cm for cod and 47.9 cm for haddock.

Diel Activity

The number of observed cod and haddock (both responding and not responding) increased at dawn and decreased at dusk in both periods (Fig. 1A, B). At night the activity was low, especially for cod. In September, cod showed two peaks of activity, one in the morning and one in the afternoon, and a period of low activity at noon. In December, there was only one peak of activity. Haddock exhibited a less clear activity rhythm during daytime. In September, haddock were active both in the morning and afternoon, without a clear decrease at noon. In December, activity decreased at noon, and there was no clear peak later. The number of responding fish followed the same trends as the number of observations of fish of each species (Fig. 1C, D).

The proportion of cod that responded was lower at night when the activity was low (from 20:00 to 6:00 in September and from 18:00 to 8:00 in December) than during the day. Of the total number of observed cod, 5% responded at night and 11% during the day (pooled data, binomial test, $p<0.001$). For haddock the difference was not significant (46% responded at night and 55% during the day, $p>0.10$).

Activity in Relation to Current Velocity

Currents in the area depended on the tides, with a maximum current velocity occurring every 6th hour in two alternating directions (southwest and northeast). The velocity range was 0–27 cm/s.

Current velocity influenced activity of the fish (Table 2). Fewer cod and haddock were observed when currents exceeded

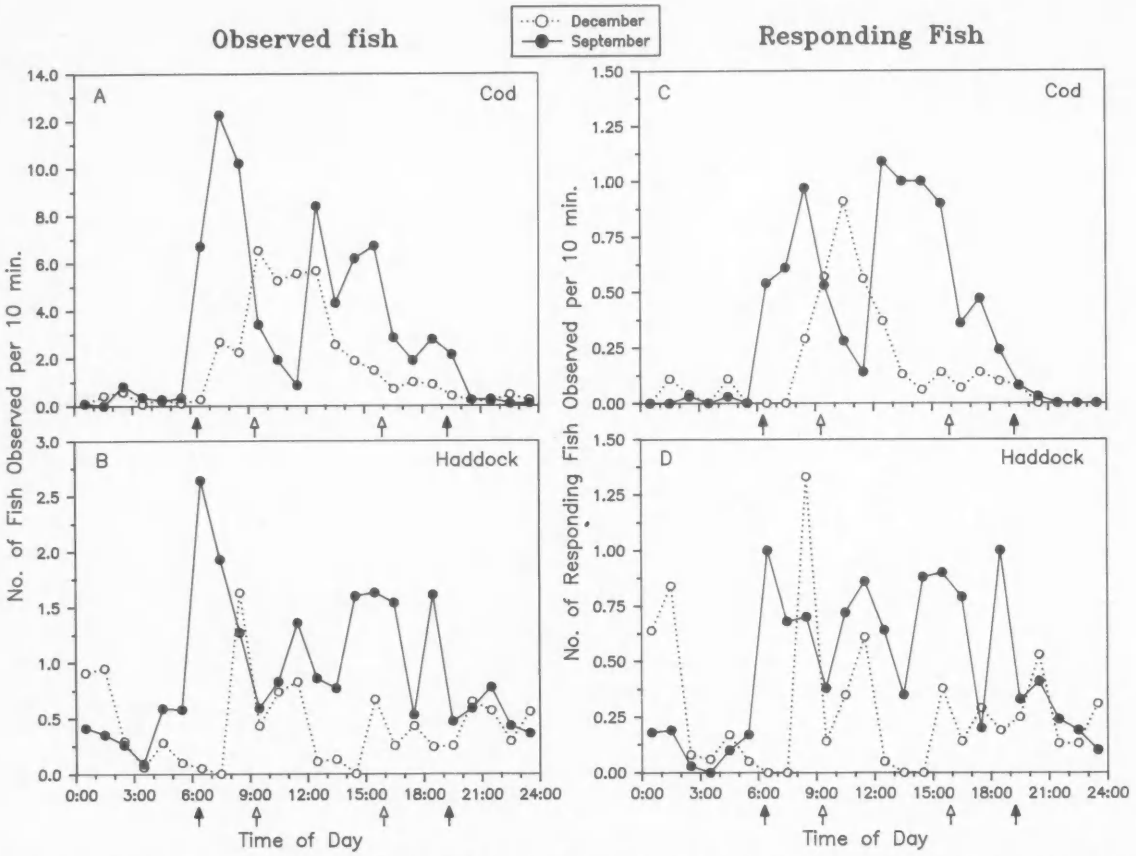

FIG. 1. Diel activity of cod (A and C) and haddock (B and D) in December 1983 (open circles) and September 1984 (solid circles). A and B, mean number of all observed fish; C and D, fish responding to bait. Mean number per 10 min is given for each hour of the day. Arrows indicate sunrise and sunset in December (open) and September (solid).

TABLE 2. Mean number of fish observed in 10-min intervals at four classes of current velocity in September 1984. Periods of high activity (more than three cod and one haddock observed per 10-min intervals; see Fig. 1A and B) and low activity are treated separately.

Species	Level of activity	Current velocity 9cm/s) 0.0–5.9	6.0–11.9	12.0–17.9	>17.9	p χ^2
Cod	Low	0.7	0.6	0.7	0.4	NS
	High	8.8	8.4	7.6	2.6	<0.001
Haddock	Low	0.9	0.5	0.5	0.2	<0.001
	High	1.5	1.9	1.7	0.5	<0.01

TABLE 3. Percentage of fish swimming in different directions relative to the current. Results are given for responding and not responding fish. Values in brackets are number of observed fish.

Species	Responding	Swimming direction Up-current	Down-current	Across-current
Cod	No	64.1 (297)	12.1 (56)	23.8 (110)
	Yes	83.7 (118)	8.5 (12)	7.8 (11)
Haddock	No	52.4 (11)	9.5 (2)	38.1 (8)
	Yes	97.2 (239)	1.2 (3)	1.6 (4)

17.9 cm/s than in periods with slower current. Variations in current velocity below 18.0 cm/s appeared not to influence activity. These trends were found both for periods of high and low activity (see Table 2).

Swimming Direction Relative to Current

Table 3 shows the swimming direction of the fish relative to the current. The majority of cod, whether responding or not, and the majority of responding haddock swam upstream (chi-square test, $p<0.001$). Haddock not responding seldom showed a straight swimming direction, and few fish were therefore categorized in this group. Responding fish more often swam upstream than not responding fish ($p<0.05$ for cod, $p=0.055$ for haddock).

Behaviour towards the Mackerel Bait

The typical behaviour of both cod and haddock when first observed was to swim slowly just above the bottom. Cod, especially, were often observed swimming with the barbel and the tips of the pelvic fins trailing over the substrate. Cod often swam

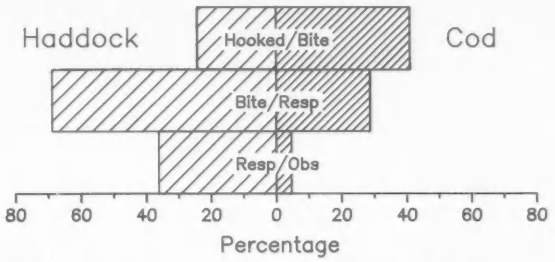

FIG. 2. Behaviour of haddock and cod towards mackerel bait. The percentages of observed fish responding to the bait, of responding fish biting the bait and of biting fish being hooked are shown.

in small shoals of 5–20 fish, whereas haddock usually appeared individually.

Of the total number of observed haddock, 36% responded to the mackerel bait, and of these 69% responded with a bite (Fig. 2). A behaviour sequence by haddock (Fig. 3A) was usually initiated by an incomplete bite, complete bites seldom occurring (Table 4). A brief taste was sometimes observed before the incomplete bite. The fish then made a rush or one to three rapid jerks of low intensity, and the bait was usually pulled out when the snood was stretched. Some jerks proceeded into a rush of low intensity, and 27% of the rushes led to hooking.

Haddock that were not hooked often made a new behaviour sequence towards the same or another bait (311 haddock made 808 behaviour sequences). A haddock could make a total of 25–35 behaviour sequences lasting more than 15 min. Several sequences included only an approach or a taste, but one haddock was observed to do 16 sequences including jerk and/or rush without being hooked. Each sequence was of short duration, and the haddock was swimming around most of the time.

Based on the number of bites, the hooking probability for haddock was 0.11 (calculated as the ratio between number of hooked fish and number of bites, 52/456; see Table 4). The probability of being hooked was twice as high in September (42/284 = 0.15) as in December (10/172 = 0.06; binomial test, $p<0.01$).

Cod responded significantly less frequently to the mackerel bait than haddock (5% of the observed cod; binomial test, $p<0.001$; Fig. 2). Cod also less frequently bit the bait (29% of the responding fish; $p<0.001$), and tasting with no further responses was more common in cod than in haddock (Table 4). A typical behaviour sequence by cod started with a taste or complete bite (Fig. 3B). The fish then often made a pull while chewing on the bait or remained still while chewing. Occasionally it made one or more jerks and/or a rush. The sequence was terminated by hooking or the bait being pulled out of the mouth.

Cod rarely made more than one behaviour sequence, and only four fish were observed to make a bite more than once. Occasionally, a cod approached or tasted a few times in succession (a total of 150 behaviour sequences were made by 136 fish).

The jerks and rushes were of higher intensity in cod than in haddock. Cod often paused briefly between each strong response while remaining stationary or moving slowly ahead with the bait in the mouth. The sequences were therefore of longer duration than for haddock.

Responses by cod were often initiated by a struggling haddock that had just been hooked. There could be long periods with no cod or few cod observed, but immediately after hooking of a haddock 10–12 cod often appeared with several cod responding. Of the total number of cod hooked on mackerel bait, 50% were hooked while another fish was making an intense response as jerk or rush. Attacks by cod towards hooked haddock were also observed.

The hooking probability for cod was 0.37 (16/43; see Table 4), significantly higher than for haddock (binomial test, $p<0.001$). The probability of being hooked was 52% higher in September than in December (13/32 = 0.41 and 3/11 = 0.27, respectively; $p>0.10$).

Discussion

Both cod and haddock exhibited a diurnal rhythm in activity, most pronounced in cod. Activity increased at dawn and decreased at dusk in correspondence with the seasonal photoperiod. The activity rhythm of cod changed from two peaks (morning, afternoon) in September to one peak at noon in December. Similar shifts between one and two peaks of activity have been observed in the response of whiting towards baited hooks (Fernö et al. 1986) and in laboratory studies on diurnal rhythms in several fish species (Müller 1978).

The low activity at night may be caused in part by a vertical migration off the bottom, observed in both cod and haddock (Beamish 1966). The low activity around noon cannot, however, be explained in this way. Furthermore, the large number of haddock observed at night indicated that this species did not migrate vertically during the periods of observation. In addition, a lower proportion of the observed cod and haddock responsed to the baits at night than during the day. The diel rhythm in activity could thus be a reflection of variations in feeding motivation.

For both species the number of observed fish and the hooking probability were higher in September than in December. This may reflect a seasonal variation in feeding activity. In cod, food intake (Rae 1967) and the response strength to bait (Solemdal and Tilseth 1984) are low during the spawning period, and this period of low feeding activity has been shown to include December (Solemdal 1984).

The general tendency of the fish to swim upstream, and the stronger tendency of responding fish to swim upstream towards the bait, indicate that the feeding activity is stimulated chemically. The observed trailing of the barbel and pelvic fins over the bottom is known to be evoked by food odours (Brawn 1969; Pawson 1977). Upstream movement towards olfactory stimuli has also been observed by others (Sutterlin 1975; Valdemarsen et al. 1977; Wilson and Smith 1984; Bjordal 1986; Fernö et al. 1986), and the importance of chemical stimuli in feeding behaviour of various species of fish is well known (Atema 1980).

The swimming activity of both cod and haddock decreased in periods of strong current. This cannot be an effect of the diel rhythm in that the same tendencies were found in periods of both high and low activity during the 24-h cycle. Furthermore, the tidal cycle is displaced about 40 min each 24 h, and during an observation period of 9 d, high and low current velocities were relatively evenly distributed throughout the 24-h cycle.

The low activity in periods of strong current may be related to energy optimization (Weihs 1987). If a fish swims predominately upstream to the food source, it would be energetically advantageous to be active during periods with moderate or low

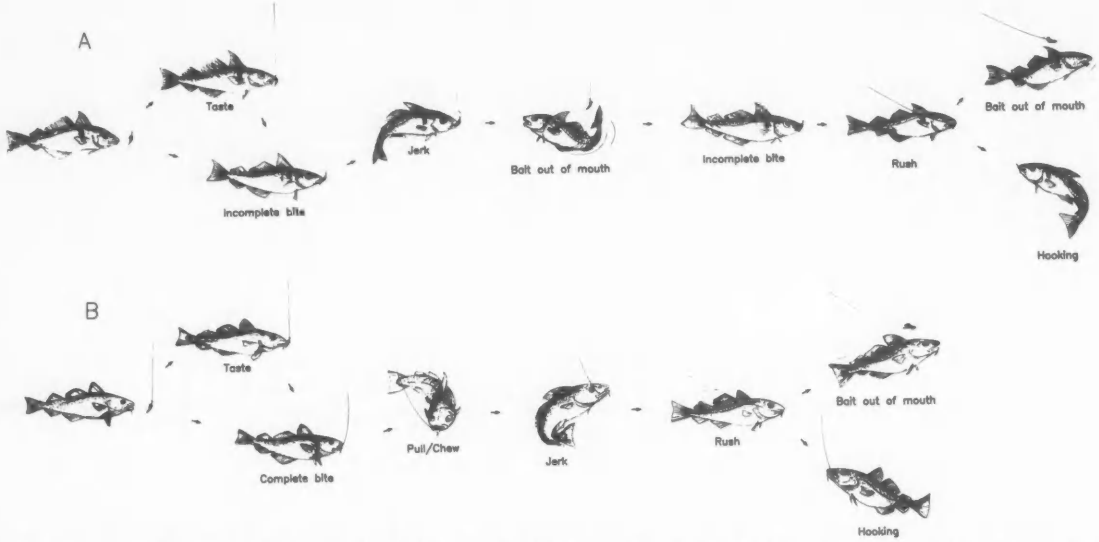

FIG. 3. Comparison between the behaviour of haddock (A) and cod (B) towards mackerel bait, indicating alternative beginning and ending behaviours.

TABLE 4. Frequency of behaviour patterns of haddock and cod towards mackerel bait, as a percentage of all responses by the fish.

Species		Behaviour patterns[a]											
		A	T	T+	InB	CoB	C	P	J	S	R	BoM	Hok
Haddock	No.	48	327	143	447	9	1	9	422	11	190	404	52
	Percent	2.3	15.9	6.9	21.7	0.4	0.0	0.4	20.5	0.5	9.2	19.6	2.5
Cod	No.	24	87	20	5	38	12	15	35	4	24	27	16
	Percent	7.8	28.3	6.5	1.6	12.4	3.9	4.9	11.4	1.3	7.8	8.8	5.2

[a]A, approach; T, tasting not followed by other behaviour pattern; T+, tasting followed by other behaviour pattern; InB, incomplete bite; CoB, complete bite; C, chew; P, pull; J, jerk; S, shake; R, rush; BoM, bait out of mouth; Hok, hooking.

current velocities and to stay in shelter when the current is strong. It was once observed that fish maintained position by heading upstream close to a platform leg. Attraction of fish to artificial reefs is well known (Unger 1966; Hastings et al. 1976), and has also been shown for offshore installations in the North Sea (Valdemarsen 1979). One reason for the aggregation of fish around such installations may be that they give shelter from the current.

Low swimming activity in periods with strong current may alternatively be due to stronger dilution of the bait odour. At higher current velocities the concentration of attractive chemical stimuli in the odour plume becomes more diluted (Olsen and Laevastu 1983). At the same time, however, the odour plume expands and dissipates faster and therefore "activates" a larger area. Because activity was similar at current velocities up to 18 cm/s, a significant effect of odour dilution is not supported by this study.

The behaviour of fish in relation to a baited longline may be divided into four phases: attraction, attacking, acceptance, and hooking. Haddock and cod showed differences in three of these phases. The attraction of fish from a distance could not be observed in this study, but in the near field there was a clear difference between the species with 36% of observed haddock responding to the mackerel bait compared with 5% for cod. Of the responding fish, 69% of the haddock and 29% of the cod bit. This means that nearly 20 times as many haddock as cod that appeared in the camera field bit the bait. When first accepting the bait, however, cod showed a more intense response with a higher probability of getting hooked than haddock.

The difference in behaviour between the species when biting the bait may partly be explained by a difference in mouth size. Haddock were generally smaller in size and have relatively smaller mouths; their behaviour consisted mainly of incomplete bites. Cod most often sucked the whole bait into the mouth (complete bite). In laboratory studies, cod have been observed to make incomplete bites very often, but this was regarded as a conditioned response due to prior experience with the baited hook (Huse 1979; Fernö and Huse 1983). After biting, both haddock and cod made jerks and rushes, but the responses of cod were more intense. These differences, particularly in regard to biting, could explain the difference in hooking probability between cod and haddock.

The different responses of the species may be explained by their different foraging behaviours. The prey of cod, such as fish, is active (Jones 1978; Casey et al. 1986). Active prey may demand responses of high intensity, but such responses should

be relatively selective. Haddock prefer slow-moving or benthic prey (Jones 1978; Cranmer 1986), which require less selective responses of lower intensity.

Cod were observed to occur in shoals, and the struggling of a hooked fish often stimulated others to respond to the baited hooks. Cod were also observed to respond to baits that were protruding outside the mouth of hooked fish. In the laboratory, cod have been observed to rapidly approach other feeding fish (Brawn 1969). This behaviour may enable them to feed more efficiently than solitary individuals (see also Brawn 1969; Pitcher 1986). This group response could partly explain the patchy distribution of hooked cod along a longline (Johannessen 1983).

The observations in this study explain findings from fishing trials with different bait sizes and hook designs. Decreasing bait size has been shown to considerably increase the catch rate for haddock, whereas the results for cod were not consistent (Johannessen 1983). A small bait increases the probability of the fish biting the hook. Smaller bait size could, on the one hand, increase the hooking probability for haddock. Cod can, on the other hand, take larger baits into the mouth, and the bait size will not influence the hooking probability to the same degree. Improved hook design also improves catches of haddock more than of cod (Skeide et al. 1986).

In conclusion, for species biting at parts of the bait, and consequently with most hookings taking place in the jaw (Skeide et al. 1986; Løkkeborg1987), the parameters of bait size and hook design are important for improving the catch efficiency of a longline. For species more often swallowing the bait (Løkkeborg 1987), and consequently having a higher hooking probability, bait size and hook design will have less influence upon catching efficiency. For such species, like cod, a bait that effectively triggers biting and swallowing is perhaps more crucial than gear design in the overall efficiency of the longline.

Acknowledgements

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Upstream Transport of Mirex by Migrating Salmonids[1]

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Scrudato, R. J., and W. H. McDowell. 1989. Upstream transport of mirex by migrating salmonids. Can. J. Fish. Aquat. Sci. 46: 1484–1488.

Mirex is a persistent chlorinated hydrocarbon found in appreciable concentrations in sediments and pelagic organisms of Lake Ontario. Concentrations are particularly high in introduced salmonids, which spawn in considerable numbers in tributaries of the Lake. We sampled the sediments and biota of several tributary streams in the Salmon River drainage basin. Greater concentrations of mirex were found in the resident brown trout (*Salmo trutta*) of tributaries accessible to migrating salmonids than in a nearby reference tributary inaccessible to migration. No significant differences in mirex concentrations were found in lower trophic levels (crayfish and stoneflies) or sediments, although mirex was detected in all samples. Because point sources of mirex are distant from these tributaries, we conclude that migrating salmonids make a significant contribution to the upstream transport of mirex from Lake Ontario. Ingestion of salmonid eggs by brown trout, decomposition of salmonid carcasses by blowfly larvae, and ingestion of carcasses by aquatic and terrestrial scavengers are all means by which the contaminant is introduced to upstream environments.

Le mirex est un hydrocarbure chloré persistant que l'on retrouve en concentration assez élevée dans les sédiments et les organismes pélagiques du lac Ontario. Les concentrations de mirex sont particulièrement élevées dans les salmonidés introduits, lesquels frayent en grand nombre dans les tributaires de ce lac. Nous avons pris des échantillons de sédiments et d'espèces vivantes dans plusieurs tributaires du bassin hydrologique de la rivière Salmon. Les concentrations en mirex observées dans les truites brunes vivant dans les tributaires accessibles aux salmonidés en migration étaient supérieures à celles observées dans les truites brunes vivant dans un tributaire de référence voisin où ne peuvent aller les salmonidés. De plus, les échantillons de sédiments ou ceux qui ont été prélevés aux niveaux trophiques inférieurs (écrevisses et perles) dans les deux tributaires, bien que contenant tous du mirex, n'ont montré aucune différence significative. Puisque les sources ponctuelles de mirex sont éloignées de ces tributaires, nous concluons que les salmonidés en migration jouent un rôle important dans le transport du mirex provenant du lac Ontario dans les tributaires de ce lac. L'introduction de ce contaminant dans les rivières se fait par le biais de l'ingestion des oeufs de salmonidés par les truites brunes, la décomposition des carcasses de salmonidés par les larves de calliphoridés et l'ingestion des carcasses par les nécrophages aquatiques et terrestres.

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Mirex, a highly persistent, chlorinated compound used primarily as a pesticide and fire retardant, was first detected in Lake Ontario fishes in 1974 (Kaiser 1974). Because of its lipophilic character, mirex accumulates in the fatty tissues of vertebrates. It is a potential human carcinogen (NAS 1978), and reduces reproductive success in various vertebrates (e.g. Ware and Good 1967; Hyde et al. 1973). The presence of mirex in the Lake Ontario ecosystem is attributed to discharges of the compound by Occidental Corporation (formerly Hooker Chemical and Plastics Corporation) into the Niagara River, and by Armstrong World Industries into the Oswego River (Kaiser 1978). Since 1974, mirex has been found in bottom sediments downstream from these sources (Holdrinet et al. 1978; Scrudato and DelPrete 1982).

During the late 1970's and early 1980's, the average body concentrations of mirex in Lake Ontario salmonids were consistently above the United States Food and Drug Administration (USFDA) limit of 100 μg/kg wet weight, and an advisory against eating these fish remains in effect (NYSDEC 1987). Mirex concentrations in Lake Ontario fishes range from 10 to 900 μg/kg on a wet weight basis and have not substantially decreased during the past decade (Sloan 1987).

Despite early controversy regarding the importance of direct versus dietary uptake of chlorinated hydrocarbons in aquatic organisms (e.g. Harrison et al. 1970; Hamelink et al. 1971), recent research indicates that dietary uptake is the primary source of these compounds in higher trophc levels where continuing discharges are not involved (Thomann 1981; Thomann and Connally 1981; Merna 1986). Eggs deposited by spawning salmonids are a primary food source for resident trout in streams of the Great Lakes (Johnson and Ringler 1979a; Merna 1979, 1986; Low 1983). Merna (1986) demonstrated that resident fish in Lake Michigan tributaries that are accessible to spawning salmonids contained elevated PCB concentrations, evidently due to ingestion of contaminated salmon eggs. Because Lake Ontario salmon eggs contain mirex (Low 1983; Lewis and Makarewicz 1988), resident brown trout (*Salmo trutta*) and other aquatic organisms in tributaries accessible to spawning salmonids may accumulate the compound by ingesting these eggs.

[1]Contribution No. 46 of the Research Center, State University of New York College at Oswego and Contribution No. 23 of the Great Lakes Research Consortium.

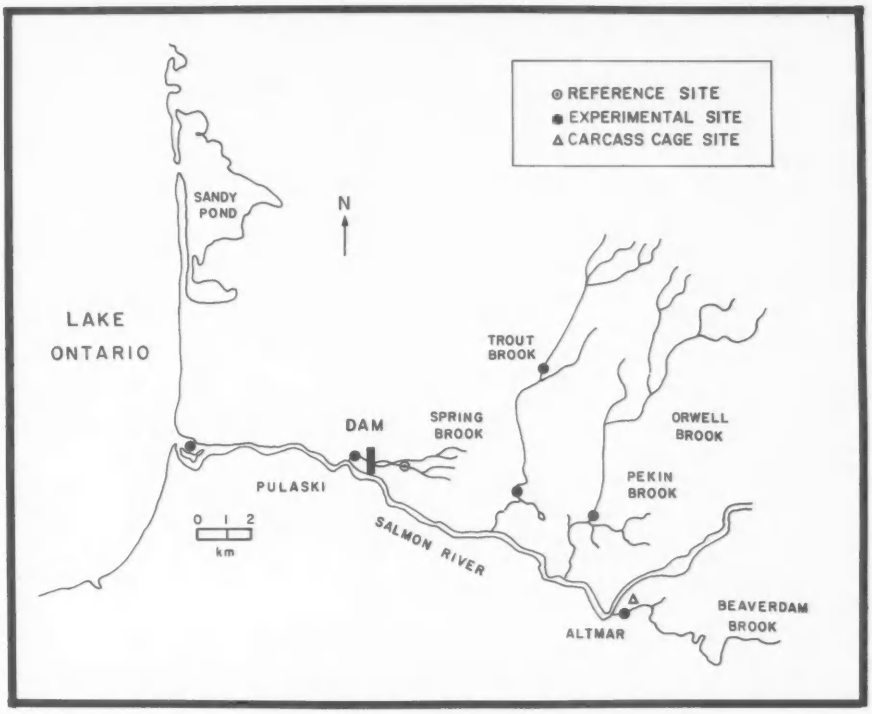

FIG. 1. Map of the study site on the eastern shore of Lake Ontario.

Mirex may also be transferred by scavenging and decomposing organisms feeding on contaminated salmon carcasses.

The objective of this study was to assess the transfer of mirex from Lake Ontario salmonids to aquatic and terrestrial organisms in Lake tributaries by measuring mirex concentrations in resident aquatic organisms and larval blowflies (Diptera: Calliphoridae), a primary terrestrial decomposer of salmonid carcasses (Fisher 1981).

Methods

Study Site

Three second and third order streams within the Salmon River drainage system, which empties into eastern Lake Ontario, were selected as study sites (Fig. 1). The Salmon River drainage is a major spawning site for anadromous fishes from the Lake, and contains New York State Department of Environmental Conservation (NYSDEC) Altmar Fish Hatchery, the primary United States salmonid hatchery on Lake Ontario. The two experimental streams (Trout and Orwell Brooks) are open to migration; Spring Brook, closed to upstream migration because of a weir and barrier dam, was selected as a reference site. Analysis of water quality and benthic community data showed no major differences in indicator variables among the three streams (Low 1983).

The study streams, located in Oswego County, are in the Tug Hill Transitional (THT) ecological zone of northern New York State (Will et al. 1982); almost 75% of the THT land base is in forest, brush, or wetlands. There is no major industrial activity in the region, and poor soils limit large-scale agriculture (Will et al. 1982). Sport fishing associated with the Lake Ontario salmonid fishery is increasing in economic importance to the area.

Collections

At Trout and Orwell Brooks, coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon were collected during October and November 1981; rainbow trout, including steelhead (*Oncorhynchus mykiss*) were collected during March and April 1982. Migratory salmon were also collected from the Salmon River estuary, the Spring Brook weir, and the Altmar Hatchery (Fig. 1). Sediments and stream-resident brown trout, crayfish (*Cambarus spp.*), and stonefly nymph populations were sampled during both collection periods from all three streams.

Fish were collected with a 400 V DC/pulsed backpack electroshocker designed by the NYSDEC. Sediment samples from depositional areas in each stream were collected by hand in 0.5-L jars. Additional sediment samples from the Salmon River estuary were obtained with a Ponar sampler.

Blowfly larvae were obtained from salmon carcasses set in open mesh cages on NYSDEC property adjacent to the Altmar Hatchery. A pooled sample of 20–30 g of larvae from each carcass and the soil below it was collected 3 wk after carcass placement and frozen for later analyses.

Laboratory Procedures

Standard fillets (NYSDEC 1979) were collected from each fish species and frozen for subsequent analyses. Eggs were taken from female salmon and frozen. Salmon carcasses used for blowfly colonization were refrigerated until needed. Stom-

TABLE 1. Mean concentrations of mirex in samples taken from Salmon River tributaries allowing upstream migration of salmonids ("experimental") and a tributary not allowing migration ("reference"), fall 1981 and spring 1982. All values micrograms per kilogram dry weight.

	Experimental sites			Reference site		
	Mean	SD	*n*	Mean	SD	*n*
Lake-run salmonids	573	262	56	—	—	—
Salmonid eggs	114	38	22	—	—	—
Blowfly larvae	365	283	33	—	—	—
Sediments	0.08	0.03	8	0.06	0.05	4
Crayfish	6.8	7.8	21	2.4	1.7	7
Stonefly larvae	2.9	1.8	16	3.9	7.7	6
Brown trout	100	85	23	3.6	9.7	14

ach contents of resident brown trout were removed and preserved in 10% formalin.

Fish samples were defrosted and coarsely ground with a Hobart food blender and dried with a Virtis benchtop freezedrier. Lyophilized samples were then reground to a fine powder in a Thomas/Wiley Intermediate Mill and mixed. One-gram aliquots were extracted for 30 s in 30 mL hexane with a Brinkman Polytron Ultrasonic Homogenizer. Polytron extraction procedures were repeated on the residues and the two extracts were combined to a working volume of 100 mL with hexane. Ten-millilitre aliquots were withdrawn and evaporated to dryness for lipid analyses. The remaining 90 mL were concentrated to 1.0 mL for Florisil cleanup.

Sediment samples (25 g) were extracted for 30 min in 100 mL of 1:1 acetone:hexane with continuous stirring, rinsed with hexane and concentrated to 1.0 mL for Florisil cleanup. Concentrated samples were eluted through a 2% deactivated Florisil column (10 g overlain by 2 g anhydrous sodium sulfate in a 10-mm inside diameter column) with 55 mL of hexane; the eluant was collected and concentrated to 0.5 mL under an N_2 atmosphere.

A Perkin Elmer Sigma 3B gas chromatograph with ^{63}Ni electron capture detector and autosampler was used for all mirex analyses. The capillary column was 25 m with a stationary phase of OV-101; injection volume was 1.5 μL. Detector temperature was 300°C, injector 250°C, and column temperature was ramped from 160 to 200°C at 5°/min. The detection limit was 1 μg/kg and the quantitation limit was approximately 2.5 μg/kg for biological samples; for sediments, detection and quantitation limits were 0.01 and 0.025 μg/kg, respectively.

Duplicate extractions were conducted on approximately 13% of the samples collected. For 28 biological samples with an average mirex concentration of 274 μg/kg dry weight, the difference between replicate analyses averaged 20 μg/kg. For a subset of six samples containing low mirex concentrations (<6 μg/kg), the difference averaged 2.99 μg/kg. All mirex standards were prepared from samples provided by Analabs, Inc.

Analysis of variance was used to analyze differences among most sample locations and sample types. For some samples, data were not normally distributed, and nonparametric tests were employed.

Results

Several biotic components of the Salmon River ecosystem contained elevated levels of mirex (Table 1). Fillets from migrating salmonids exhibited the highest mean concentration

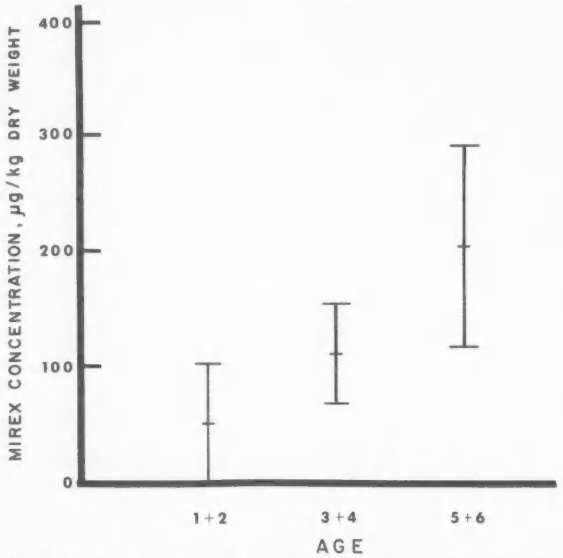

FIG. 2. Mirex concentration (micrograms per kilogram dry weight) in resident brown trout as a function of age in streams accessible to migrating salmonids. Age classes were combined for the analysis. Numbers of trout in each age class were 8, 12, and 3 for trout 1–2, 3–4, and 5–6 yr old.

(573 μg/kg), followed by blowfly larvae collected from the salmonid carcasses (365 μg/kg), eggs from migrating salmonids (114 μg/kg), and fillets from brown trout collected in experimental streams (100 μg/kg).

No significant differences in mirex concentrations in standard fillets or eggs were detected among species of migrating salmonids (ANOVA, $p>0.05$), thus, the means reported for these variables are for lake-run salmonids overall. Neither egg lipid content nor mirex concentrations in standard fillets of the fish from which eggs were collected explained a significant amount of the mirex detected in those eggs (regression analysis, $p>0.05$).

Fillets of resident brown trout from the experimental streams contained an average of 100 μg mirex/kg dry weight, significantly greater than the average (3.6 μg/kg) detected in conspecifics from the control stream (one-sided Mann–Whitney test, $p<0.05$). Although significant differences in mirex concentrations were observed among crayfish, stoneflies, and sediments (Mann–Whitney test, $p<0.05$), no differences were observed between experimental and reference streams for these three sample types. Mirex concentrations were often near the limits of analytical detection for these samples.

Mirex-contaminated salmonid eggs comprised a large proportion of the diets of resident brown trout in the experimental streams. Of 16 trout with food in their stomachs when collected in Orwell and Trout Brooks, 75% contained salmon eggs in spring and 62% contained them in fall. Mirex levels in fillets of resident brown trout from the experimental streams increased with age (ANOVA, $p<0.05$; Fig. 2), suggesting that long-term bioaccumulation of mirex from food sources is occurring. No such increase was observed in trout from the reference stream.

No significant relationship was observed between mirex concentration and lipid content in fillets of resident brown trout ($p>0.05$, regression analysis) from the experimental streams.

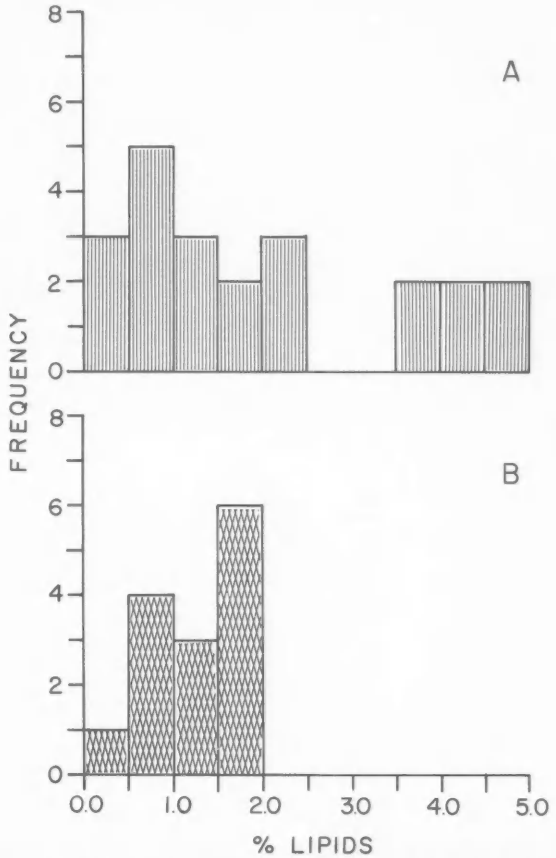

FIG. 3. Frequency distribution of the percentage lipids (wet weight basis) in fillets of resident brown trout from tributaries accessible to salmonid migration (A) and Spring Brook (B), which is not accessible to migrating salmonids.

Lipid content of resident brown trout was significantly higher in the experimental streams than the reference stream (t-test, $p<0.05$; Fig. 3). In Orwell and Trout Brooks, lipid content of trout was 2.1% of total wet weight; in Spring Brook, lipids averaged 1.3%. When normalized for lipid content, the difference in mirex concentrations between trout of reference and experimental streams was still substantial. Trout from Orwell and Trout Brooks averaged 1.2 μg mirex per gram lipid, while those from Spring Brook averaged 0.07 μg/g.

In addition to observations of the introduction of mirex into the aquatic food chain of the Salmon River basin, transfer of the compound to the adjacent terrestrial food web was also observed. Concentrations of mirex in blowfly larvae averaged 365 μg/L, second only to salmonid carcasses in mirex content.

Discussion

Anadromous fish appear to be a major vector for transporting mirex to resident aquatic organisms in the Salmon River drainage basin. Resident brown trout in tributaries of the Salmon River accessible to migrating salmonids probably assimilated mirex by ingesting contaminated anadromous fish eggs, a major food source during salmonid migrations (Johnson and Ringler 1979a). Ingestion of blowfly larvae (Johnson and Ringler 1979b) which had fed on decomposing salmonid carcasses may also have resulted in mirex transfer to resident trout. Direct uptake from stream water appears to be an unlikely source of the elevated mirex concentrations observed in these trout. Although we have no direct measurements of stream water concentrations, sediment concentrations were not significantly different in reference and experimental streams, making it unlikely that concentrations in overlying water would differ. Thus, we conclude that dietary uptake is the most important pathway resulting in contamination of resident brown trout in Orwell and Trout Brooks.

Mirex is not readily metabolized in fish (Pritchard et al. 1973; Zitko 1980), which explains the steady accumulation of mirex in older brown trout.

Mirex is being transferred to the terrestrial community as well as the aquatic. Blowfly larvae are contaminated by feeding upon salmonid carcasses (Table 1), and it is likely that adults, which would disperse throughout the basin, would also be contaminated. Mammals, birds and other scavengers feeding on fish carcasses would provide additional vectors by which the contaminant could be distributed throughout the drainage basin and adjacent watersheds.

Airborne transport of mirex from the lake to downwind ecosystems is a plausible explanation for the presence of mirex in the reference stream. Atmospheric transport is a major vector for PCB deposition in the Great Lakes (Murphy 1984), and preliminary sampling indicates that measurable concentrations of mirex are present in air masses moving across Lake Ontario (J. Hassett, State University of New York College of Environmental Science and Forestry, pers. comm.). Terrestrial scavengers might also transport mirex from one basin to another. The large differences in mirex concentrations in resident brown trout in reference and control streams, however, demonstrate the importance of migrating fish in the transport of contaminants to upstream ecosystems.

Although significant contamination of resident brown trout has been observed in this study, levels of mirex do not exceed the USFDA action limit (100 μg/kg wet weight). The average concentration of 100 μg/kg dry weight reported in Table 1 for fish collected in 1981–82 is equivalent to approximately 25 μg/kg wet weight, well below the action level. The highest concentration observed, 80 μg/kg wet weight, was also below the USFDA action limit. Because of the possibility of additional accumulation of mirex in upstream ecosystems, periodic monitoring of resident organisms is warranted.

Our data on stomach contents of brown trout corroborate those of earlier studies (e.g. Johnson and Ringler 1979a,b) which indicate that salmon eggs are a heavily-used food of resident trout in the Salmon River drainage. Increased fat content of resident brown trout in streams accessible to migrating salmonids also indicates that salmonids are important in the stream's food web. Migrating salmonids may provide direct (e.g. eggs), or indirect energy subsidies through enhanced primary and secondary production. These fish are known to be important in the phosphorus cycle of other streams (Richey 1975) and may be important in this area as well. Our observation that fat content is higher in streams accessible to migrating salmonids corroborates the results of Johnson and Ringler (1979a), who observed higher condition factors for resident brown trout in these streams.

The contribution of migratory salmonids to parts of the food web other than fish appears to be less significant. Neither sed-

iments, crayfish, nor stoneflies showed significantly increased concentrations of mirex in experimental streams compared with the reference stream. This suggests that either migrating salmonids do not represent a major energy input to the benthic food web, or that mirex is metabolized or excluded from crayfish and stoneflies. Because previous workers have shown that crayfish do accumulate mirex in laboratory studies (De la Cruz and Naqvi 1973), minimal ingestion of salmonid eggs or carcasses probably explains the low mirex concentrations observed in these benthic invertebrates. For crayfish in the experimental sites, the high standard deviation in mirex concentration (Table 1) suggests that the extent to which individual crayfish consume salmonid eggs or carcasses may vary considerably.

Salmonid migration and spawning links upstream and downstream ecosystems, and must be recognized as a factor when assessing the transport of contaminants in the Lake Ontario basin (Lewis and Makarewicz 1988). Mirex represents only one of the contaminants in Lake Ontario salmonids. Photomirex, PCBs, and other contaminants are also being transferred to upstream terrestrial and aquatic ecosystems by salmonid migration, although the extent to which they accumulate in resident biota is unknown.

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Production of Freshwater Invertebrate Populations in Lakes[1]

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Plante, C., and J. A. Downing. 1989. Production of freshwater invertebrate populations in lakes. Can. J. Fish. Aquat. Sci. 46: 1489–1498.

This research draws together data on the secondary production of 164 invertebrate populations in 51 lakes to test the hypothesis that the annual production of aquatic invertebrate populations is significantly correlated with the mean annual population biomass, individual body mass, and ambient temperature. Further analyses examine the effects of water chemistry, trophic status, and lake morphometry. Mean annual biomass, individual body mass, and the mean annual water temperature accounted for 79% of the variance in the logarithm of annual secondary production. In contrast to the findings of previous studies, the ratio of mean annual production to mean annual biomass ($P/\bar{B}$) varied systematically with population biomass. No significant difference was found between the secondary production of littoral and open water invertebrate populations. Analyses also suggest that zoobenthic and zooplanktonic populations of similar biomass, body mass, and temperature have similar rates of secondary productivity. Analyses demonstrate that the total phosphorus concentration in the water column, and other trophic indicators were positively correlated with secondary production. The pH, lake depth, thermocline depth, drainage area, and the water turnover rate were also found to be correlated with the secondary productivity of natural populations of lentic invertebrates.

Ce travail réunit des données de production annuelle de 164 populations d'invertébrés aquatiques pour tester l'hypothèse que la production annuelle est significativement corrélée avec la biomasse moyenne annuelle des populations, la masse individuelle des animaux et la température de l'eau. D'autres analyses examinent l'effet des caractéristiques chimiques de l'eau, du niveau trophique de même que la morphométrie des lacs. La biomasse moyenne annuelle, la masse individuelle maximale et la température moyenne de l'eau de surface contribuent pour 79% de la variance du logarithme de la production secondaire annuelle. Contrairement à ce qui apparait dans les travaux antérieurs, le rapport entre la biomasse moyenne et la production annuelle ($P/\bar{B}$) varie systématiquement avec la biomasse. Il n'y a pas de différence significative entre la production secondaire des populations du littoral et celles de la zone pélagique. L'analyse suggère aussi que pour une biomasse, une taille individuelle et une température de l'eau semblables, les populations d'invertébrés benthiques et planctoniques ont des productions et des biomasses semblables. Les analyses démontrent que la concentration du phosphore total de la colonne d'eau et d'autres indicateurs trophiques sont positivement corrélés avec la production secondaire. Le pH, la profondeur des lacs, la profondeur de la thermocline, la superficie du bassin de drainage et le taux de renouvellement de l'eau sont aussi corrélés avec la production secondaire des populations naturelles d'invertébrés aquatiques.

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The measurement of rates of growth and production of natural animal populations has been a major preoccupation of ecologists throughout this century (e.g. Boysen-Jensen 1919). Winberg (1971), for example, has suggested that the development of a general theory of biological productivity is one of the central aims of contemporary biology. Rates of secondary production vary widely in nature and are affected by a variety of biotic and abiotic characteristics of the environment. Although secondary production has now been measured for many different organisms in many kinds of environments, we do not yet know which factors are most closely correlated with secondary production or the normal quantitative relationship between secondary production and the characteristics of the environment. Such knowledge would find theoretical application in the trophodynamic analysis of ecosystems (Lindeman 1942) and practical application in resource management and the detection of pollution (Downing 1984a).

Many factors have been hypothesized to affect the productivity of invertebrate populations in aquatic ecosystems (reviewed by Downing 1984a), yet quantitative tests for relationships between production and many of these factors are rare. Ecologists have found, however, that production is correlated with population biomass (e.g. Waters 1977), so that factors affecting the biomass of populations should also influence the rate of secondary production. Population production is therefore often expressed as the annual production to biomass ratio ($P/\bar{B}$) in hopes of yielding standardized production values that can be compared among species or populations with differing biomasses. Early studies of respiration and more recent empirical research on various other groups of organisms (reviewed by Dickie et al. 1987) suggest that individual body mass should influence these $P/\bar{B}$ ratios. The additional effect of temperature on secondary production can be inferred from knowledge of its

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influence on rates of growth (e.g. Vijverberg 1980), egg development (e.g. Bottrell 1975), population increase (e.g. Armitage et al. 1973), and feeding (e.g. Zimmerman and Wissing 1978). Other variables such as food availability (e.g. Jónasson 1978) and ecosystem primary productivity (e.g. Brylinsky 1980) might further influence secondary production.

No one has yet considered the combined effect of biological variables and environmental characteristics on the productivity of natural populations, and no synthesis of invertebrate secondary production data from lake ecosystems has been attempted. Little is known, for example, about the relationship between aquatic secondary production and eutrophication, lake morphometry, geography, and climate or whether littoral populations are more or less productive than those in open water. Such knowledge would aid ecological theoreticians by identifying the degree and form of postulated correlations between secondary production and characteristics of natural ecosystems, and improve the management of aquatic ecosystems by providing quantitative predictions of secondary production in natural and managed lakes.

The purpose of this research is to draw together data on the secondary production of diverse populations of lentic invertebrates, to test the hypothesis that the annual production of these aquatic invertebrate populations is significantly correlated with their population biomass, body mass, and physical characteristics of the environment. The results of this work permit us to test several hypotheses advanced in recent publications regarding the effects of water chemistry, trophic status, and morphometric characteristics of lakes on the production of resident aquatic invertebrate populations.

Methods

Data on the annual production of freshwater invertebrate populations in lakes (P, grams dry mass per square metre per year) were collected from published surveys (Table 1). Attendant data were also gathered on the mean annual population biomass ($\bar{B}$, grams dry mass per square metre) and maximum individual body mass (W_m, milligrams dry mass) of each population, and on biological, morphometric, physical, and chemical characteristics of the water bodies. Where data on environmental characteristics were not published, such data were compiled through direct communication with the authors of production studies. The populations considered here consist primarily of species and genera of rotifers, crustaceans, insects, annelids, and molluscs, but taxonomic levels depend upon the degree of detail presented by the authors of each study. A few of our populations therefore consist of families or classes. The published production data were originally derived using several different estimation procedures. Only production rates estimated as the product of general production to biomass ratios ($P/\bar{B}$) and $\bar{B}$ were rejected a priori since such indirect measures would include unwanted imprecision (Rigler and Downing 1984). Data on the production of stream invertebrates were not included in the analysis because of radical physical differences between lotic and lentic environments.

Variable Definitions and Computation

The term "production" here connotes the annual production of biomass by a population, including somatic growth and mortality. If a publication presented production data for more than one year, or used more than one computation method, we recorded the average of available data. Likewise, if production values were reported for several stations or areas in a water body, a mean value was computed because data on variables such as temperature were seldom available for specific sites. Production values, although sometimes averages (i.e. $\bar{P}$), are abbreviated as P for annotational simplicity.

The effects of several independent variables were tested in a multivariate analysis of the annual production of invertebrate population (Table 2). Among these variables are the population biomass, individual body mass, and several biological, chem-

TABLE 1. List of the lakes for which secondary production data were obtained. N is the number of population production estimates obtained for each water body.

Water body	Latitude	Longitude	N
Bob Black Pond	34°19′N	84°52′W	2
Broa Reservoir	22°00′S	49°18′W	1
Char Lake	74°04′N	94°53′W	6
Dock Lake	45°N	84°W	1
Eglwys Nunydd Reservoir	42°26′N	3°28′W	16
Federsee	48°09′N	9°40′E	1
King George VI Reservoir	51°17′N	0°26′E	1
Lac de Port-Bielh	42°30′N	0°10′E	7
Lake Akulkino	67°N	33°W	3
Lake Chad	13°40′N	14°E	6
Lake Cundare	38°06′S	143°37′E	1
Lake Esrom	56°99′N	12°14′E	5
Lake George	0°00′	30°12′E	1
Lake Hayes	44°59′S	168°49′E	1
Lake Kasumigaura	36°N	140°15′E	5
Lake Kinneret	32°49′N	35°22′E	1
Lake Krivoe	65°N	35°E	8
Lake Krugloe	65°N	35°E	5
Lake Manitoba	51°N	98°8′W	6
Lake Maljøen	63°15′N	10°26′E	4
Lake Memphremagog	45°00′N	72°15′W	3
Lake Mikołajskie	53°N	21°22′E	4
Lake Mýtvatn	65°22′N	6°35′E	2
Lake Nakuru	0°22′S	36°05′E	3
Lake Naroch	54°52′N	26°27′E	1
Lake Norman	35°26′N	80°30′W	7
Lake Ontario	43°45′N	78°W	6
Lake Ototoa	36°31′S	174°44′E	1
Lake Sibaya	27°20′N	32°24′E	1
Lake Taltowisko	53°N	22°E	4
Lake Werowrap	38°14′S	143°30′E	1
Lake Zelenetzkoye	67°N	33°W	4
Loch Leven	56°10′N	3°30′W	9
Marion Lake	49°18′N	122°33′W	2
Mirror Lake	43°57′N	72°W	3
North Twin Lake	42°16′N	85°25′W	1
Øvre Heimdalsvatn	61°27′N	8°43′E	3
Pääjärvi	61°04′N	25°08′E	2
Pink Lake	38°06′S	143°37′E	1
Pyramid Lake	52°55′N	128°W	1
Queen Elizabeth II Reservoir	51°17′N	0°26′E	1
Queen Mary Reservoir	51°25′N	0°17′W	1
Red Lake	58°02′N	36°18′E	9
Savanne Lake	48°50′N	90°06′W	1
Shallow Lake	45°N	84°E	1
Slotermeer	53°N	5°30′E	1
South Twin Lake	42°16′N	85°25′W	1
Texas Pond	33°12′N	97°10′W	3
Tjeukemeer	52°50′N	5°30′E	4
Waldsea	52°17′N	105°12′W	1
West Lost Lake	42°16′N	85°25′W	1

TABLE 2. Independent variables used for correlation analysis of the annual secondary production of invertebrate populations. Chlorophyll, phosphorus, nitrogen, and calcium concentrations, secchi disc depth, pH, and temperature, are annual averages. Abbreviations in text are indicated if used. Total solar radiation is for 1 yr and the maximum is for the highest month. N_1 is the number of observations, and N_2 the number of lakes represented.

Variable	Symbol	Units	N_1	N_2	Range	Median
Mean population biomass	$\bar{B}$	$g \cdot m^{-2}$	164	51	0.0005–23.7	0.17
Maximum individual mass	W_m	mg· dry mass	137	50	0.00002–582	0.14
Chlorophyll	*Chl*	$\mu g \cdot L^{-1}$	63	18	0.225–4099	35
Total phosphorus	*TP*	$\mu g \cdot L^{-1}$	72	16	0.27–9850	13
Total nitrogen	*TN*	$\mu g \cdot L^{-1}$	71	13	0.075–20	0.65
Secchi disc depth		m	106	36	0.09–13.7	2.8
Calcium		$mg \cdot L^{-1}$	102	30	1.29–316	13
pH			135	39	5.7–10.5	7.8
Water temperature	T	°C	164	51	1.5–26	13.8
Depth, mean	Z	m	160	47	0.5–86	5.3
maximum	Z_m	m	148	40	1.4–244	12.5
Area of body of water	*Area*	km^2	160	49	0.009–19 684	1
Drainage area	*Dra*	km^2	83	27	0.1–70 448	40
Thermocline depth	Z_t	m	64	19	0.9–14.3	7.6
Latitude		°N or S	164	51	0–74.5	48.5
Altitude		m	92	31	−208–2285	213
Turnover rate of water		yr^{-1}	81	17	0.09–13.5	1.1
Air temperature	T_{air}	°C	164	51	−16.2–22.7	8.9
Maximum solar radiation	Rad_m	$kcal \cdot cm^{-2} \cdot yr^{-1}$	164	51	60–220	110
Total solar radiation	Rad_t	$kcal \cdot cm^{-2} \cdot yr^{-1}$	164	51	11.5–22	15

ical, and physical characteristics of lakes considered by the ecological literature to have a significant bearing on freshwater productivity (review by Downing 1984a).

The population biomass was computed as the average annual standing stock of each population. In some Polish and Soviet studies (Winberg et al. 1973; Alimov et al. 1972; Andronikova et al. 1970; Hillbricht-Ilkowska and Weglenska 1970), the mean annual biomass was estimated from growing season mean biomass, assuming biomass values of 0 for the winter months, since it is, in reality, very small (Alimov et al. 1972). The benthos data (e.g. insect larvae) given in these studies were not analyzed because the benthos biomass during the winter months cannot be assumed insignificant (Cablancq and Laville 1972).

Individual body mass was most readily obtained as the maximum individual body mass (milligrams dry mass), usually calculated from the largest length class using length–mass relations given in summary publications (e.g. Bottrell et al. 1976). Other estimates of maximum body mass were taken from growth curves. Mean values of maximum body mass of congeners were used in some cases where species-specific data could not be found.

Measures of trophic conditions such as chlorophyll, nitrogen, and phosphorus concentrations in the water bodies were obtained as annual averages. Mean annual water temperature was read from figures if unavailable, per se, in the publications. Exact water temperature data were not available for all water bodies. Because of the obvious physiological importance of temperature, we used an empirical equation based on latitude (Straškraba 1980) to estimate the mean annual surface water temperature where otherwise unavailable. Solar radiation data were obtained from maps (Budyko 1974), and air temperatures were taken from tables of long-term averages (Wernstedt 1972). Characteristics of the water bodies were usually measured during the year in which the production estimates were made. If simultaneous data were unavailable, data from the nearest available year were substituted. A few annual production and mean annual biomass values were converted to grams dry mass employing the conversion factors given in the publications themselves or by using general conversion factors (Cummins and Wuycheck 1971; Winberg et al. 1971).

Statistical Analysis

Stepwise least squares multiple regression analysis was used to determine the relationship of annual population production to the characteristics of populations and environments. Logarithmic transformation was applied to production and biomass values, chlorophyll, nitrogen, and phosphorus concentrations, and some morphometric factors, to eliminate heteroscedasticity and linearize the relationships. Only variables with significant ($p<0.05$) partial effects were retained.

Not all measures of population and environmental characteristics were available for each production estimate. No attempt to interpolate missing variables was made. Only cases where all independent variables were available could be analyzed by multiple regression, therefore multiple regression analysis was only performed to examine the relationship between secondary production, population biomass, temperature, and individual body mass in order to retain a large number of cases. The relationships between other variables and secondary production were subsequently examined by an analysis of correlations between the residuals of this multiple regression equation and less frequently available independent variables. The relationship between lake zonation and secondary production was investigated using an analysis of covariance (Gujarati 1978).

Results and Discussion

Estimates of the annual production and biomass of 164 aquatic invertebrate populations, drawn from 51 lakes, reservoirs, and ponds were obtained, covering a wide geographical range (Table 1). The range of ecological conditions in the sur-

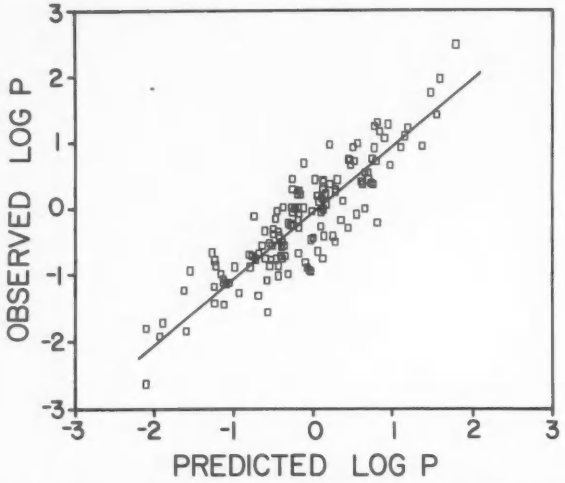

FIG. 1. Relationship between the logarithm of annual production (log P) predicted by equation 1 and the observed logarithm of P for aquatic invertebrate populations. P is expressed in grams dry mass per square metre per year. The line represents a 1:1 relationship.

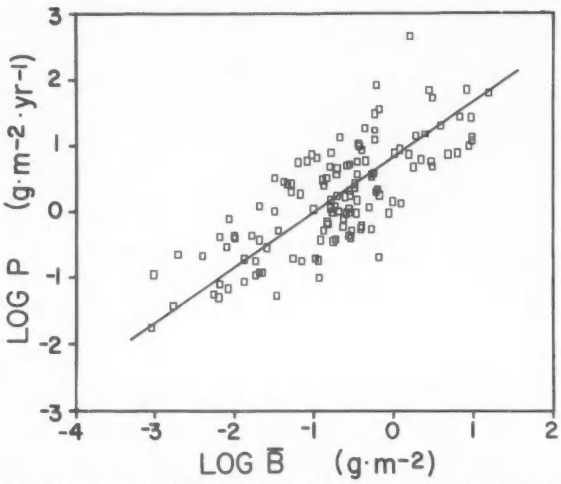

FIG. 2. Relationship between the logarithm of annual production (log P; grams dry mass per square metre per year) and the logarithm of mean annual biomass (log $\bar{B}$; grams dry mass per square metre) of aquatic invertebrate populations. $P = 5.33\ \bar{B}^{0.73}$, $R^2 = 0.63$, $N = 164$, $p < 0.001$.

veyed water bodies brackets much of the range existing in known lakes (Table 2). A full listing of the data and data sources is available at a nominal charge from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ontario, Canada, K1A 0S2.

The secondary production of freshwater invertebrate populations (P) was significantly correlated with the annual mean population biomass ($\bar{B}$; grams dry mass per square metre), maximum individual body mass (W_m; milligrams), and the surface temperature (T, °C) by the equation:

$$(1)\quad \log(P) = 0.06 + 0.79 \log(\bar{B}) - 0.16 \log(W_m) + 0.05\,T,$$
$$N = 137;\ R^2 = 0.79;\ F = 165;\ p < 0.001.$$

The partial F-values of all independent variables indicate that each accounts for a significant ($p < 0.001$) portion of the variability in log(P). Several other good multiple regression equations were also found (Plante 1987) but this one had normally distributed residuals and the highest coefficient of determination (R^2). This equation shows that the logarithm of production can be predicted with 79% precision (Fig. 1). The absolute value of the residuals of equation 1 ranged from 0.004 to 0.96 (median 0.28), indicating that prediction errors, in untransformed form, are as little as 0.9% but in some cases as great as an order of magnitude. Median prediction errors of P are around −50% and +100%. Although annual biomass is the most important variable, a further significant degree of variability in log P was accounted for by the body mass of the organisms and the temperature of the water.

Biomass

As has been found for other faunae, we found that B was the most important correlate of population production and had a strong positive effect on P. A regression using only log $\bar{B}$ as a predictor explains 63% of the variance in log P (Fig. 2). This is not surprising because for short intervals of time $P = gB$, where g is the instantaneous growth rate (Rigler and Downing 1984). Thus, unless g varies as B^x, where $x < -1$, P should increase with $\bar{B}$. Such severe density dependence of growth should rarely be encountered in natural systems.

The way in which P varies with $\bar{B}$ is therefore of greater interest than the simple existence of a correlation between P and $\bar{B}$. Several authors have suggested, for example, that annual secondary production of different populations can be estimated employing an average production to biomass ratio ($\overline{P/B}$) as a constant (see Rigler and Downing 1984 for a review). Such a procedure would be invalid if $P/\bar{B}$ were to vary systematically with $\bar{B}$. The regression coefficient for log $\bar{B}$ in equation 1 is significantly smaller than 1 ($p < 0.05$) indicating a nonlinear relationship between P and $\bar{B}$. We therefore found $P/\bar{B}$ to decline with $\bar{B}$ on average. This finding contradicts the analysis of Banse and Mosher (1980) who found no correlation between $P/\bar{B}$ and $\bar{B}$ after the use of body mass as a covariable. An explanation for this discrepancy could be that Banse and Mosher (1980) excluded the part of the year spent in resting eggs or in stages with reduced growth rates in computing their mean population $\bar{B}$. Because periods of relative dormancy are shorter at low latitudes and high temperature, their computation method may have yielded $\bar{B}$ that were lower than mean annual biomasses at low P, thus overestimating the slope of the log annual P to log $\bar{B}$ relationship. We used annual mean biomass measurements in our research because the "growing season" length is difficult to define and determine, and because we wished to account for environmental characteristics rather than to attempt to correct for them. The part of the year suitable for population growth is, of course, influenced by the environment. Also in contrast to our results, Humphreys (1981) found that the slope of the log P:log$\bar{B}$ relationship for aquatic invertebrates was not different from 1 when body mass was included as a covariable. He assumed an exponent of −0.25 associated with W_m. Both the research of Humphreys and Banse and Mosher are based on relatively few observations (31 and 28 cases, respectively). Our more extensive data collection indicates that the exponent of the relationship between P and $\bar{B}$ is significantly less than 1 and therefore annual $P/\bar{B}$ ratios in aquatic invertebrates are inconstant with $\bar{B}$.

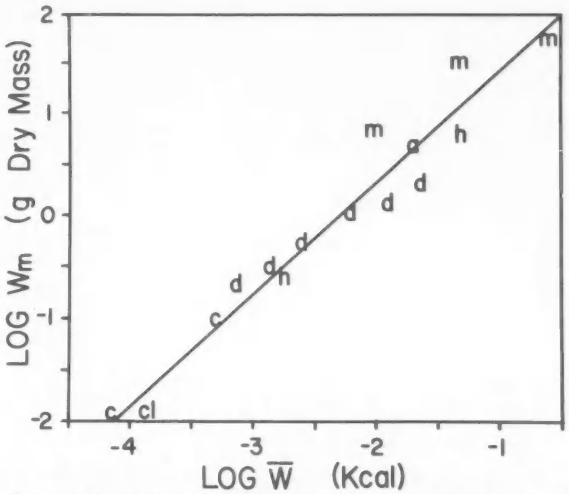

FIG. 3. Relationship between the log maximum body mass (W_m) and the log average body mass (W) of 15 populations that were common to our study and that of Banse and Mosher (1980). m, molluscs; a, annelids; d, Diptera; h, Hirudinae; c, copepods, and cl, Cladocera. The line represents the least squares regression ($W_m = 10^{2.42} W^{1.06}$, $r = 0.97$) where the exponent 1.06 is not significantly different from 1.

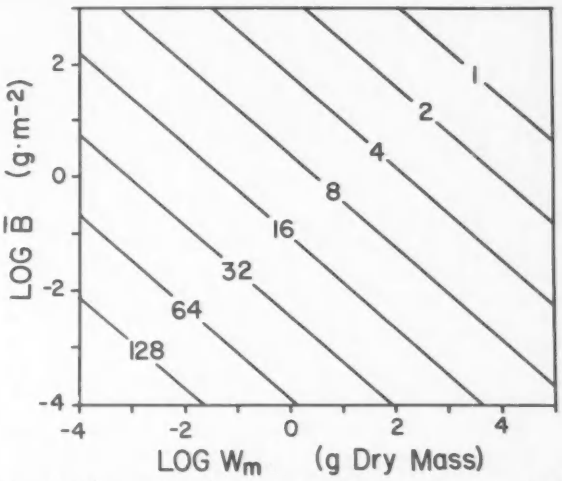

FIG. 4. $P/\bar{B}$ (annual production to mean biomass ratio; per year) of aquatic invertebrate populations predicted from equation 1, as related to the mean annual biomass ($\bar{B}$; grams dry mass per square metre per year) and maximum body mass (log W_m; grams dry mass) at a mean annual surface temperature (T) of 15°C.

It is possible that cohort $P/\bar{B}$ or $P/\bar{B}$ values calculated over the interval of active growth of a population do not vary systematically with $\bar{B}$, but even if this were true, application of such knowledge would require detailed, population-specific data on the fraction of the year spent in active growth, data which are sufficient for the direct calculation of P. The prediction of annual P using annual $\bar{B}$ avoids this difficulty.

Body Mass

Equation 1 shows that P of lentic invertebrate populations declines as $W_m^{-0.16}$ where $\bar{B}$ is entered as a covariate. This exponent is significantly greater ($p<0.05$) than the value suggested by general allometric theory. Allometric arguments suggest that the production rate of invertebrate populations should decline as $W_m^{-0.25}$ if the biomass is used as a covariate (Humphreys 1981; Lavigne 1982; Peters 1983; Calder 1984). In contrast, Banse and Mosher (1980) found that $P/\bar{B}$ varied as $W^{-0.37}$ (W = log mean adult body mass) for invertebrates, an exponent significantly lower than both our results and the theoretical value of $W^{-0.25}$. Banse and Mosher attempted to exclude the effect of the environment by restricting their analysis to environments with average annual temperatures between 5 and 20°C. Their results should therefore be comparable with ours, because we have removed the temperature effect by including it as an independent variable. They used log mean adult body mass ($\bar{W}$) as an independent variable which is related to our W_m as $W_m \propto W^1$ (Fig. 3). The difference cannot therefore be explained by the body-size measurements used.

Peters (1983) has demonstrated, however, that a range of -0.06 to -0.39 can be obtained for the exponent for the effect of body mass on secondary production, depending on the taxonomic grouping used in the regression analysis. Recomputing the $P/\bar{B}$: W regression for all the data of Banse and Mosher, Peters (1983) obtained a body mass exponent of -0.17, equivalent to the exponent that we found. Dickie et al. (1987) reanalyzed the data of Banse and Mosher (1980), adding the data on fish from Humphreys (1979) and marine benthos from Schwinghamer et al. (1986). Dickie et al. concluded that exponents fitted over many orders of magnitude of W, that pool several types of organisms, are around -0.25, and thus reflect the general physiological scaling of production. They also conclude, however, that such exponents are often < -0.25 when fitted within groups of similar sized animals (e.g. marine meiofauna, fish or terrestrial mammals). Dickie et al. (1987) believe that this difference is due to additional ecological scaling factors that are relevant within particular environments. Using the reasoning of Dickie et al. (1987), the significantly greater exponent that we obtained ($P/\bar{B} \propto W_m^{-0.16}$) might suggest that populations of freshwater lentic invertebrates might have different biomass, home range, or spatial distribution allometry than the communities that Dickie et al. (1987) examined. Such an analysis is highly speculative, however, and is based on the interpretation of differences among exponents of allometric relationships which have often been based upon small sample sizes. Whatever the reason, the larger number of cases in our study (137) shows that $P/\bar{B}$ of aquatic invertebrate populations declines as W^b where $b > -0.25$.

Figure 4 shows a predicted response surface of $P/\bar{B}$ as a function of $\bar{B}$ and W_m for temperate water bodies ($T = 15$°C). $P/\bar{B}$ can be as great as 100 for small animals with low population biomass. $P/\bar{B}$ decelerates rapidly with increased $\bar{B}$ and W_m, such that large animals with high biomass have $P/\bar{B}$ approaching 1, and are just capable of annual biomass replacement. Annual $P/\bar{B}$ in lentic invertebrate populations is thus clearly inconstant with $\bar{B}$ and W_m.

Temperature

Our analyses show that the production of aquatic invertebrate populations is positively correlated with temperature. The literature suggests that temperature should have a positive effect on secondary production because growth rates (Vijverberg 1980), development rate (e.g. Vijverberg 1980), and feeding

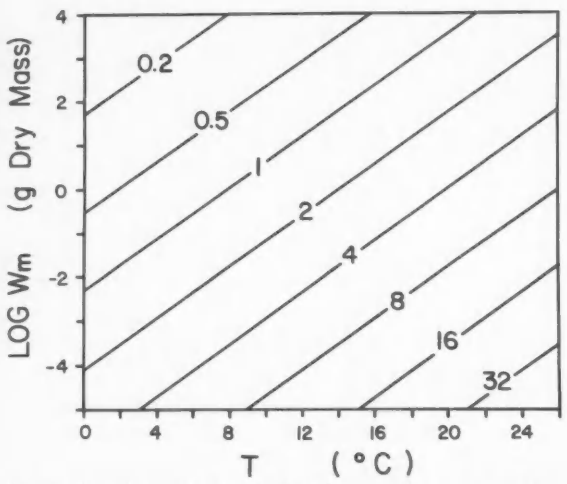

FIG. 5. Annual secondary production (P; grams dry mass per square metre per year) of aquatic invertebrate populations predicted from equation 1, as related to the maximum body mass (W_m; grams dry mass) and mean annual surface temperature (T; °C) for a population with a mean annual population biomass of 300 mg·m^{-2}.

rates (see Peters 1984) increase with temperature and may combine to allow organisms in warmer climates to form increased numbers of cohorts annually. In contrast, Banse and Mosher (1980) suggest no temperature dependence of annual invertebrate $P/\bar{B}$ within the range of 5 to 20°C. Again, this may be due to differences in biomass computation employed by these authors in an attempt to correct for the effect of environment on secondary productivity. Winberg (1972) has suggested that comparisons of annual $P/\bar{B}$ values may be difficult because they vary with the length of the growing season. Water temperature is correlated with growing season length and its use as a covariate in our equations avoids the estimation of growing season length, per se, providing an unbiased evaluation of the statistical correlation of temperature and annual secondary production.

Figure 5 suggests that changes in temperature, working through the intermediaries of growth rate, development rate and voltinism, may have a profound effect on production rates. Our analysis shows that an increase in temperature from around 0 to 24°C is correlated with an increase in P of more than an order of magnitude. As suggested by many authors (e.g. Johnson 1974; Jónasson 1978; Humpesch 1979; Vijverberg 1980; Marchant and Hynes 1981; Sutcliffe et al. 1981), in situ growth rates of freshwater invertebrate populations are generally correlated with temperature conditions. The dependence of invertebrate secondary production on temperature has been anticipated by the physiological literature, but has never before been demonstrated empirically.

Other Factors Correlated with Freshwater Secondary Production

Data on several important environmental characteristics were not available frequently enough in the literature to permit their entry into multiple regression analyses, but are of great enough theoretical importance to merit individual analysis. The effect of these factors was therefore evaluated by examining their correlations with the residuals of equation 1 (Table 3). This procedure is conceptually equivalent to the next step beyond equation 1 in a stepwise multiple regression analysis, employing forward selection variable entry (Hocking 1976).

TABLE 3. Pearson correlations between the characteristics of the water bodies and the residuals of equation (1). The variables are those of Table 2. *indicates $p<0.05$, **indicates $p<0.01$ and ns indicates $p>0.05$.

Variable	r and significance
Turnover rate	0.31**
Z_t	0.26**
log *TP*	0.23*
log *Chl*	0.21*
pH	0.20*
Rad_m	−0.20**
Z_m	0.14*
Rad_t	−0.14^{ns}
Z	0.13^{ns}
Log *area*	0.11^{ns}
Ca	0.09^{ns}
log *TN*	0.08^{ns}
Altitude	−0.08^{ns}
log *Dra*	0.07^{ns}
Latitude	0.05^{ns}
Secchi	−0.04^{ns}
T_{air}	−0.001^{ns}

Secondary production must ultimately be limited by the primary productivity of an ecosystem (Edmondson 1974). Variables correlated with the trophic status of ecosystems should therefore show positive correlations with secondary production. Some analyses based on limited data (Kajak and Dusoge 1970; Dermott et al. 1977; Makarewicz and Likens 1979; Brylinsky 1980) have suggested such correlations, but evidence has been contradictory (c.f. Pederson et al. 1976). Our analyses show that the residuals of equation 1 were positively correlated with the annual average chlorophyll concentration of the water column (Table 3), a commonly used indicator of aquatic ecosystem primary productivity. This result is echoed by analysis of correlations between residuals and annual mean total phosphorus concentration, probably because phosphorus is the primary element limiting to algae growth in lakes (Dillon and Rigler 1974; Smith 1982) and primary production (e.g. Brylinsky 1980). The residuals were also positively related to the water renewal rate (Table 3), another correlate of the lake trophic status (Vollenweider and Dillon 1974), and with the amount of solar radiation received at the water surface, probably due to direct reliance of aquatic invertebrate populations on phytoplankton productivity. Correlations with these trophic indices uphold the theoretical view that aquatic secondary production is ultimately limited by rates of primary productivity.

The residuals of equation 1 were positively correlated with the pH. This result agrees with Brylinsky's (1980) work on phytoplankton, and upholds the negative effect of low pH on benthic invertebrate biomass suggested by the work of Roff and Kwiatkowski (1977). Our analysis detected a significant correlation of secondary production with pH, even though our observations were made in lakes that varied only within the relatively benign pH range of 5.7 to 10.5. This result may explain the observation that certain species of fish in acidified lakes appear to starve to death even though the pH is within physiologically tolerable limits (e.g. Mills et al. 1987). We found that low pH was generally associated with decreased secondary production of their major food source.

TABLE 4. Analysis of the residuals for the effect of habitat (benthic versus planktonic) on aquatic invertebrate population production. The covariates were mean annual biomass, mean annual surface temperature, and maximum body mass. Analysis of variance was performed using the residuals of equation 1 as the dependent variable.

Group	Mean residuals	N
Plankton	0.144	59
Benthos	−0.008	77
$F=5.21$	$p=0.024$	

The theoretical literature suggests that several morphological characteristics of lakes might have indirect effects on rates of secondary production of invertebrate populations. For example, several authors (e.g. Johnson 1974; Matuszek 1978; Brylinsky 1980) have suggested that benthos production in shallow lakes is greater than that of deep lakes. In spite of this, Table 3 shows that the residuals of equation 1 were positively correlated with maximum depth of the lakes. This effect is probably correct for planktonic populations, but when we analyzed the benthic populations alone (not shown) our data show the expected significant ($p<0.05$) negative relationship between the residuals and Z_m. Table 3 shows that thermal stratification, which is related to morphometry, also affects the production of invertebrate populations. The residuals of equation 1 were positively correlated with thermocline depth, agreeing with the less comprehensive work of Brylinsky (1980).

Similarity of Production Patterns among Lake Zones

The planktonic and benthic habitats are quite different and these differences have long been thought to influence the relative production of zooplanktonic and benthic invertebrates. Empirical test of this idea has heretofore been impossible due to a lack of knowledge regarding the quantitative effect of the covariables $\bar{B}$ and W_m on the secondary production of lentic invertebrate populations. Analysis of the residuals of equation 1 indicates that zooplanktonic populations may be slightly more productive than zoobenthic populations of equivalent biomass, body mass, and temperature (Table 4). Although zoobenthic populations are subject to frequent anoxic conditions that could have a negative effect on their productivity, the best explanation for this difference may be that T does not always estimate the temperature experienced directly by the populations for which production is estimated. T was most often available as the mean surface temperature, and because water temperature usually decreases with depth in lakes, benthic populations are generally colder than planktonic animals. This difference could cause the benthic populations to appear less productive for a given T. The residuals indicate that zooplanktonic P is about 40% higher than zoobenthic P for given $\bar{B}$, W_m and T, a difference easily explained by the effect of temperature gradients.

Benthic invertebrates in the littoral zone have long been thought to be more productive (Kajak and Dusoge 1975a,b, 1976) and have higher $P/\bar{B}$ ratios (Holopainen 1979) than invertebrates found in other zones, although some conflicting evidence exists (e.g. Jónsson 1985; Eaton 1983). We therefore used analysis of covariance to test the hypothesis that the zone in which invertebrate populations were collected had a significant effect on the rate of secondary production. The data were sorted into three categories: data which appeared to represent the entire water body, data collected only from the littoral zone, and those collected only in the pelagic zone. There were 17 pelagic populations and 24 littoral populations. An analysis of covariance on P using $\bar{B}$, T, and W_m as covariates was employed to test for the effect of zonation on secondary productivity. Table 5 shows that no significant effect of zonation on secondary productivity of either planktonic or benthic invertebrates could be demonstrated. The surprisingly high rates of production often observed in the littoral zone (e.g. Kajak and Dusoge 1975a,b) probably result only from higher invertebrate biomasses and temperatures in littoral regions, and not from higher proportional rates of productivity. This finding explains the anomalous results of Eaton (1983) who found that production rates of *Chaoborus* were nearly six times higher in the profundal than in the littoral zone. $\bar{B}$ of Eaton's *Chaoborus* in the littoral zone was much lower than in deep water, while $P/\bar{B}$ was equivalent in the two zones.

TABLE 5. Analyses of covariance for the effect of zonation on aquatic invertebrate population production. The covariates were mean annual biomass, mean annual surface temperature, and maximum body mass for benthos, and mean annual biomass, mean annual surface temperature, for plankton. N here is the number of secondary production estimates included in the analyses.

Zone of the water body	Coefficients	t-significance
	Planktonic populations	
Littoral	−0.08	0.16
Pelagic	−0.033	0.51
	$N=79$	
	Benthic populations	
Littoral	0.09	0.17
Pelagic	−0.02	0.74
	$N=77$	

General Discussion

Ecological research throughout this century has provided much information on the production of various invertebrate populations in aquatic ecosystems. Published empirical generalizations thus far have shown that cohort (Waters 1977) and annual (Banse and Mosher 1980) production rates rise with population biomass, and that body size (e.g. Banse and Mosher 1980), voltinism, and life span (Waters 1977) may influence the relationship between P and $\bar{B}$. No multivariate synthesis of the mass of data available on lentic invertebrates has previously been attempted. Previous production analyses have only been bivariate, an approach which has oversimplified the complexity of production processes.

Our analyses uphold the results of other researchers working with other groups of organisms (e.g. Banse and Mosher 1980; Dickie et al. 1987) in demonstrating a very strong general relationship between annual production, annual mean biomass, and individual body mass of aquatic invertebrate populations. We have also identified several additional covariates, including water temperature, and correlates of ecosystem productivity that account for ecologically important variation in P. Log $\bar{B}$, for example, explains 63% of the variation in log P in equation 1, but half of the remaining variance in P in equation 1 is explained by W_m and T. More than 80% of the variation in log P could be explained by simple characteristics of the population and habitat (Tables 3 and 4). This is especially encouraging given the imprecision of the variables entering into production calculations (Rigler and Downing 1984; Downing 1984b), and

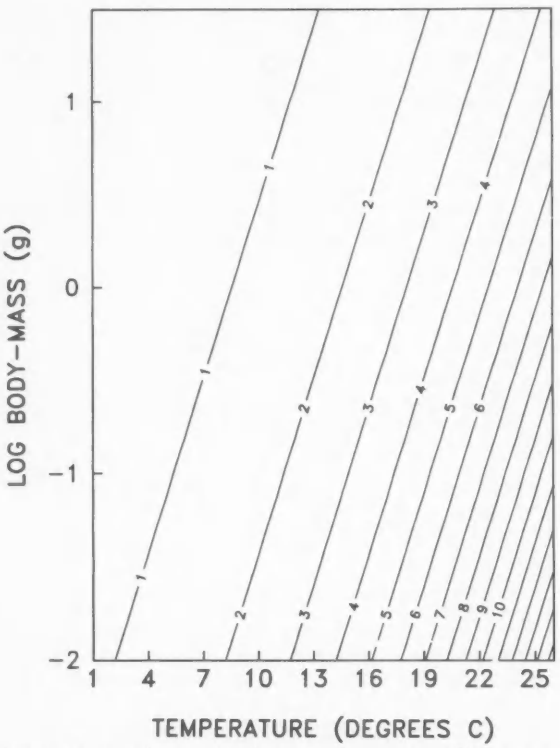

FIG. 6. Number of nonoverlapping generations per year (G), as related to the maximum body mass (W_m; grams dry mass) and mean annual surface temperature (T; °C) for an hypothetical benthic population with a mean annual population biomass ($\bar{B}$) of 0.1 $g \cdot m^{-2}$. The number of generations is estimated using equation 2.

indicates new directions for future freshwater secondary production research.

Some variables, although well represented in the available data (Table 2), could account for no further significant variation in secondary production (Table 3). For example, nitrogen concentration, suggested by many (e.g. Smith 1982) to have a significant effect on the primary production of aquatic ecosystems, was uncorrelated with the residuals of equation 1, underlining the importance of phosphorus as the primary limiting nutrient in lakes. Neither the mean depth nor the lake area were significantly correlated with the residuals, reiterating the suggestion that littoral zones yield secondary production rates similarly proportional to biomass, body mass, and temperature as in other zones (Table 5). Finally, the correlations of residuals to both latitude and altitude were insignificant, suggesting that temperature is a very important component of geographic location for the secondary production of aquatic invertebrate populations.

Equation 1 offers a pragmatic solution to secondary production estimation for populations that are too costly to investigate using traditional methods. Production measurements of cohort forming populations are conceptually simple but require repeated measures of density and body size over time (Edmondson and Winberg 1971; Benke 1984; Rigler and Downing 1984), variables that are costly to measure (Downing 1984b; de Bernardi 1984; Peckarsky 1984). The estimation of secondary production for populations not forming cohorts, or for populations with unknown age structure (e.g. almost all planktonic populations) is even more costly, because growth rates must be measured directly. Consequently, a quantitative model that links production rates to characteristics of the organisms and environment could be of great practical value. It is tempting to suggest that equation 1 might serve to estimate P, a posteriori, for continuously reproducing populations, for which $\bar{B}$ can be estimated and for which body mass is known or can be estimated. Such an approach might be useful and sufficiently precise for many purposes.

Extrapolation of our equation 1 also predicts systematic trends in life history strategies. The frequency of cohort formation is of interest in ecology both for its importance to life-history theory and for the correction of production calculations based on the size-frequency method (Benke 1984). Waters (1979) has found that cohort $P/\bar{B}$ is approximately 5, therefore equation 1 can be rearranged to yield the number of nonoverlapping generations per year (G):

$$(2)\quad \log(G) = -0.21 \log(\bar{B}) + 0.05(T) - 0.16 \log(W_m) + 0.06 - \log(5).$$

Equation 2 suggests that the number of generations per year should increase with temperature and decrease with body mass (Fig. 6). In spite of the indirect derivation of equation 2, it predicts correctly that populations of small chironomids and Ephemeropterans in a warm Texas pond (Benson et al. 1980) should be multivoltine and that chironomids in a high arctic lake like Char Lake (Welch 1976) should have very long life cycles. In addition, Fig. 6 suggests that in any environment, populations of small organisms should form more generations per year than larger ones. This suggestion is upheld by the data of Jónsson (1985) who studied the life history and production of eleven taxa of chironomids at one site in Lake Esrom. The number of generations formed per year varied between 1 and 3, among species. The species with the greatest maximum body size, *Stictochironomus histrio*, formed the smallest number of generations per year, while the smallest taxon, *Cladotanytarsus* spp., formed the largest number of generations. Jónsson's (1985) data show a significant ($p<0.05$) negative correlation between the size of an organism and the number of cohorts formed annually, precisely as predicted by equation 2. Further investigations of this phenomenon would be a promising area for future research.

Because the estimation of secondary production is important in both theoretical and applied ecology, it is important to know what variables affect rates of secondary production. Furthermore, under some conditions, predicted secondary production might be sufficiently accurate and precise, eliminating the high cost of direct measurement. Several variables have a simultaneous effect on secondary production and a large fraction of the variation in the logarithm of annual production of aquatic populations can be predicted from the mean annual biomass, mean water temperature, and maximum adult body mass alone. Future studies promise to show that systematic analysis of chemical, physical, and morphological characteristics of the environment could improve our understanding of factors limiting secondary productivity in freshwaters, as well as our capacity to predict it.

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Extrapolation of Laboratory pH Dose–Response Data to Fluctuating Environments: Comparisons with a Null Model

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Haefner, J. W., and L. C. Abbott. 1989. Extrapolation of laboratory pH dose–response data to fluctuating environments: comparisons with a null model. Can. J. Fish. Aquat. Sci. 46: 1499–1509.

A simple model was developed to extrapolate laboratory dose–response data to randomly varying conditions. We fit published data of dose–response experiments for the effects of low pH stress on survival rates of stream macro-invertebrates to a modification of the Weibull distribution. Using the resulting parameter estimates and Monte Carlo simulation, we compared the values obtained in constant laboratory conditions with the expected survival rates obtained in fluctuating environments. For each of three species, we performed 108 Monte Carlo experiments in a full factorial design that varied the mean pH, the standard deviation of pH fluctuations, the distribution from which pH values were drawn, the distributions of runs of constant pH, and the presence of episodic events. Fluctuating environments decreased the survival rates of resistant species, but increased survivorship of sensitive species. No one exposure duration under laboratory conditions could consistently be extrapolated to the suite of variable environments we examined. Probit analyses performed on the observed and simulated data indicated that LC-50s of different observed exposure durations were similar to each other and to the LC-50s of the simulated data assuming an exposure of 24 h. Based on these results, we recommend that toxicity studies incorporate temporal variability directly by using varying dose levels in laboratory tests.

Les auteurs ont élaboré un modèle simple pour extrapoler les données de laboratoire dose–réponse à des conditions variant de façon aléatoire. Des données publiées d'essais dose–réponse portant sur les effets d'un stress par pH faible sur les taux de survie de macro-invertébrés de cours d'eau ont été ajustées à une distribution de Weibull modifiée. Les auteurs ont ensuite comparé, à l'aide des paramètres obtenus et d'une simulation de Monte Carlo, les valeurs obtenues en conditions constantes de laboratoire aux taux de survie prévus en environnements fluctuants. Pour chacune des trois espèces étudiées, 108 essais de simulation Monte Carlo ont été réalisés. Ces essais comportaient une conception totalement factorielle permettant de faire varier le pH moyen, l'écart-type des fluctuations du pH, la distribution d'où les valeurs de pH avaient été tirées, les distributions des séries d'essais à pH constant et la présence d'événements épisodiques. La fluctuation des environnements avait pour effet de réduire le taux de survie des espèces résistantes, mais d'accroître celui des espèces sensibles. Aucune durée d'exposition en laboratoire n'a pu être extrapolée, de façon continue, à la série d'environnements variables étudiés. Les analyses par probit réalisées pour les données observées et simulées ont montré que les CL-50 correspondant à diverses durées d'exposition observées étaient semblables entre elles et à celles des données simulées aux durées d'exposition de 24 h. Se fondant sur ces résultats, les auteurs recommandent que l'on intègre directement la variabilité temporelle aux études de toxicité en utilisant des doses variables au cours d'essais en laboratoire.

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A common method of characterizing an organism's response to a chemical stress is by determining LD-50, LC-50, or ED-50 (Loomis 1978). While this method continues to be valuable as a screening tool, its predictive power is limited for several reasons: (a) it is a single species (most often: single population) test, (b) it is generally an acute test, (c) only a few species are examined, (d) it attempts to characterize a continuous response function by a single number and thereby requires assumptions of symmetry and normality of the organism's response, and (e) the tests are normally performed under constant, homogeneous laboratory conditions. Because of these restrictions, application of the data to natural systems has been limited. Recently, three aspects of the problem of extrapolating toxicological data to other situations have been addressed: (a) extrapolating laboratory data from one taxon to another (Suter and Vaughan 1984; Suter et al. 1983, 1985), (b) extrapolating acute tests to chronic conditions (Suter et al. 1983, 1985; Suter and Vaughan 1984), and (c) extrapolating laboratory studies of single species to effects occurring in ecosystems (O'Neill et al. 1982; Suter et al. 1985). While the above referenced studies are based on Monte Carlo analysis of standard data, Kimball and Levin (1985) have argued that it is appropriate to perform the experiments in the more realistic setting of multi-species mesocosms.

In natural environments, the levels of stressing agents fluctuate in time and space. These fluctuations can be characterized as having a frequency, duration, and intensity (Pickett and White 1985). In general, little is known about populations' responses to stress when the treatment is variable with respect to these characteristics. The successful extrapolation of laboratory dose–response studies to their ecological consequences in natural environments, however, requires that we understand

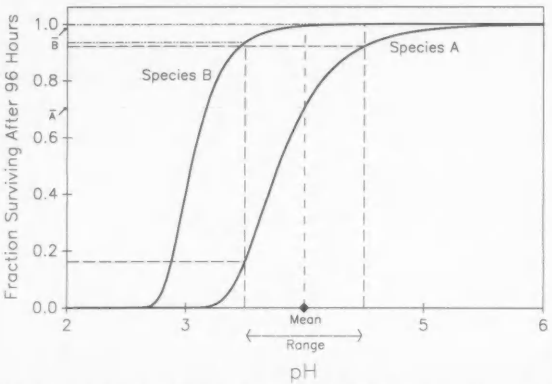

FIG. 1. Hypothetical relationship between fluctuating pH and survival in two species. Mean and range of fluctuations indicated on the abscissa. Response to dose is indicated by the heavy, solid lines for species A and B. Corresponding responses at mean pH for species A indicated by $\bar{A}$ and for species B by $\bar{B}$. Ranges of responses for both species are indicated by two pairs of dot–dash lines. Note the ranges of the responses of the two species relative to the range of fluctuations of pH. Note also the asymmetric responses around the mean responses of both species. In both species, survivorship at the mean pH is higher than the mean survivorship.

the effects and importance of fluctuations in levels of the stressors on appropriate organismal responses. This is especially relevant to the problem of predicting the effects of acid deposition when the low pH input varies temporally due to annual snowmelt events or more frequent but less intense disturbances due to rainfall (e.g. Harvey and Whelpdale 1986).

Figure 1 illustrates the effects of variable pH levels on the dose–responses after 96 h of two hypothetical macro-invertebrates (e.g. stream insects). The solid curves represent a population's survival response following exposure to constant pH for 96 h. Insect A is sensitive to pH (can only survive at high pH); insect B is relatively insensitive to pH since it can survive both low and high pH levels. Environmental variability is represented by symmetric fluctuations around the mean with the range indicated on the x-axis. If we assume that population survivorship responds quickly relative to the time scale of the environmental fluctuations, then, because of the nonlinear relationships of dose to response for the two species, the variability of survival rate can differ greatly between the species. Moreover, symmetric variations in pH can produce asymmetric, skewed response distributions. The points $\bar{A}$ and $\bar{B}$ are the species' responses at the mean pH. The indicated range of responses for the species illustrates that the time-averaged response of species A and B, given symmetric fluctuations of pH, will be lower than $\bar{A}$ and $\bar{B}$. In other words, the mean response when pH is variable is not necessarily equal to the response at the mean pH. The direction of the skew (above or below the response at the mean pH), can have subtle and important ecological consequences. Sweeney (1984) described similar ideas of Pradhan (1945) for general invertebrate life history response to temperature fluctuations.

Because of this relationship between nonlinear responses and variable stresses, extrapolating dose–response data from controlled laboratory experiments to natural systems may be statistically biased. The purpose of the research reported here was to characterize and describe the nonlinear dose–response curves similar to those depicted in Fig. 1 for three species of stream macro-invertebrates and to estimate the amount of error made when these nonlinear response functions are extrapolated to randomly varying environments.

A Monte Carlo simulation model was constructed to determine the effect of random environmental variation in daily pH values on the estimate of survivorship of the stream insects. The objective of the model was to describe the types of environmental variation at which the traditional toxicological dose–response tests fail to predict the survivorship of a population of organisms exposed to varying levels of a toxicant. In essence, we ask: how much error will be made in attempting to extrapolate survival estimates from the constant conditions of laboratory tests to naturally variable environments? Consequently, for this analysis we are concerned only with survival and ignore reproduction, competition, predation, emergence, emigration, immigration, and other ecologically relevant factors. We also assume that a population's response to stress as measured by survival rate occurs within the smallest timestep used in the model (24 h). Moreover, we further assume that previous exposure to a stressing agent for periods longer than those of the experiment does not affect survivorship. Because of these restrictive assumptions, we interpret the model as a "null" model (Harvey et al. 1983) which produces the expected distribution of survival rates when pH varies on a daily basis and individuals respond as observed under constant laboratory conditions for exposure to fixed time periods of pH.

Methods

Dose–Response Description

We fit a modified Weibull distribution to dose–response curves relating different durations of pH exposure to survivorship for 10 species of freshwater macro-invertebrates (Gaufin 1973). The cumulative Weibull distribution is:

$$(1)\quad F(s) = 1 - \exp\left(-\left[\frac{s}{b}\right]^c\right)$$

where s, b, and c are positive, and s is the independent (stress) variable, b is the "scale" parameter, and c is the "shape" parameter, although different notation is used (Srinivasan and Wharton 1975; Thoman et al. 1969; Thoman and Bain 1969; Pinder et al. 1978). When $F(s)$ is interpreted as the probability of dying, the survival function is $f(s) = 1 - F(s)$.

One method of estimating b and c is to linearize the survival function as:

$$(2)\quad \ln\left(\ln\left[\frac{1}{f(s)}\right]\right) = c\ln(s) - c\ln(b),$$

Hahn and Shapiro (1967) give details. This method works well for many data sets (Pinder et al. 1978), but not those in which there are few data points most of which are either 0 or 1. The double log function requires that these points be excluded from the parameter estimation procedure. In small data sets, exclusion of these data may result in poor estimates. This problem is reduced for a maximum likelihood estimator for b and c, which uses only a single log transform (Srinivasan and Wharton 1975). But, as described below, our particular application of the Weibull is based on discrete stress levels (pH levels) as the independent variable. These types of data are incompatible with the maximum likelihood approach.

Because of these constraints, we used an iterative, steepest-descent method that did not use derivatives. This approach

explores parameter space for the best values by iteratively changing the current choice of parameters in a direction that reduces total error (Daniel and Wood 1980). Since ths is an iterative method that uses the current best estimate to obtain the next, it must be started with an initial guess of the parameter values. We used equation (2) to obtain initial parameter estimates for equation (1). Because our data resembled curves as in Fig. 1, this produced shape estimates less than zero. Substituting negative values for c in the survival function is equivalent to fitting

$$(3)\quad f(s) = \exp\left(-\left[\frac{b^c}{s^c}\right]\right)$$

where b and c are positive, and s is the independent stress level.

In the iterative algorithm, we approximated the two-dimensional, continuous parameter space (represented by an axis for 'b' and an axis for 'c') as a discrete grid with small mesh size (0.001 parameter units). An error function was computed for the initial point obtained from linear regression and its eight neighboring points on the grid. The error function used was the χ^2 statistic obtained by comparing the observed survival distribution with that obtained using the parameter values defined by the current point on the grid being considered. The next pair of parameter estimates accepted was that point of the nine with the smallest χ^2. This process was repeated until the smallest χ^2 difference between neighboring points was less than 10^{-15}. We also implemented the estimation procedure using a search criterion to minimize the sum-of-squared residuals. Using the estimates obtained this way in a goodness-of-fit test produced larger χ^2 values than resulted from parameters obtained by minimizing the χ^2 during the search. Consequently, we used the latter technique. Since this approach to parameter estimation finds only local minima, we performed several estimations using different initial parameter quesses and different grid spacings to verify that we had achieved a global minimum (i.e. a single, local minimum). All trials converged to the same point.

We performed the estimation using 10 species and all of the exposure durations for which data were available in Gaufin (1973). For each species, we obtained Weibull curves for each exposure duration which relates pH value to the cumulative (final) survivorship at that pH and of that time period. These relationships differ from normal presentations of laboratory survivorship data, which show death rates as functions of time for different stress levels. We transformed Gaufin's (1973) data from stress-level curves over time by choosing specific time intervals (i.e. 24, 48, 72, and 96 h) for each time curve and plotted response for each stress level (pH) in the data set for each time interval selected. We also used data for long durations (approximately 40 d) for several species in Gaufin (1973).

Model Structure

After fitting the transformed dose–response data to the Weibull survival distribution as described above, three of the 10 species were used in the simulation model. These species represented three points on a continuum of responses to pH stress. *Pteronarcella badia*, a large stonefly, was chosen as a resident species. The amphipod *Gammarus lacustris*, a large scud, was used as a pH sensitive species. A smaller stonefly, *Isoperla fulva*, was selected as a species with an intermediate response.

The model manipulated five characteristics of random environments: the probability distribution from which random pH values were drawn, the mean and standard deviation of that distribution, the distribution of exposure periods (run-lengths) of pH levels, and the presence or absence of episodic events. We used three different distributions (normal, log-normal, and uniform), three mean pH values (pH 4, 5, and 6), three standard deviations of the pH distributions (0.1, 0.5, and 1.0), two types of run-length distribution (empirical and fixed), and two numbers of episodic events (0 and 36) per 365 simulated days. A complete factorial design was examined. Thus, 108 different treatment combinations were used. Each model was replicated 100 times producing 100 mean daily survivorships averaged over the duration of the simulation for each 108 treatments. The Monte Carlo analysis was repeated separately for all three species.

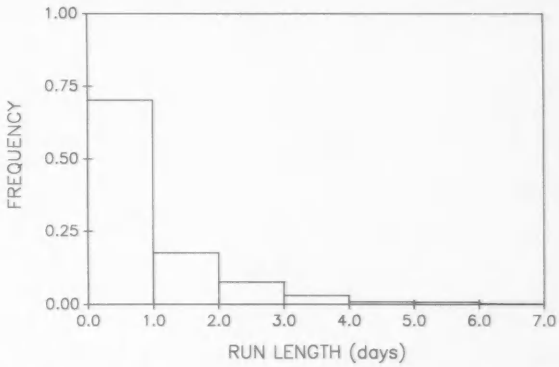

FIG. 2. Frequency distribution of days of constant pH from a time series of 854 d from seven streams in New Jersey and Pennsylvania (from USGS 1973a,b).

Random pH values were drawn from a particular type of distribution with a fixed mean and standard deviation. Random deviates were generated using standard IMSL (International Mathematics and Statistical Library) functions GGNML, GGNLG, and GGUBS for the normal, log-normal, and uniform distributions, respectively (IMSL 1982). Deviates returned from these subroutines were transformed to the appropriate mean and standard deviation of the desired pH value. If pH values so generated were less than 1.0 or greater than 13.0, they were truncated to one of these extremes. The means used in the simulations were those used in Gaufin (1973).

In order to incorporate any acclimation that might occur during longer trials (e.g. 96 h versus 24 h) and to mimic more faithfully natural fluctuations of pH in streams, we did not permit pH to change at every simulated time step. Instead, for each pH value selected we also randomly chose a duration period. For some treatments, these "run-lengths" were selected from an empirical distribution of run-lengths obtained from 854 d of pH data from seven streams in New Jersey and Pennsylvania (USGS 1973a,b). The frequency distribution of the length of these "runs," obtained by categorizing observed pH to the nearest tenth of a pH unit, was used to create an empirical "run-length distribution" is shown in Fig. 2. This distribution had a mean of 1.6 d and a range of 1–7 d. Each species was characterized by a family of curves similar to those in Fig. 1. Each member of the family defined the species' survival rate as a function of pH for an experiment performed for a particular duration (e.g. 24, 48, 72, or 96 h). With these functions, a random pH level, and a random run-length, the cumulative survivorship was computed. Thus, random survivorship is a func-

tion of both the run-length distribution and the pH distribution. To test the sensitivity of our results to this particular empirical run-length distribution, we repeated the test using a run length distribution in which all exposure periods were 24 h.

We also examined the effects of one implementation of the concept of episodic events. We investigated episodic events as relatively frequent, but mild temporary depressions in pH. We simulated episodic events by randomly selecting 36 d on which the events were to begin. At the initiation of each event, we decreased the simulated pH by 8% and linearly increased it over 6 d until it returned to the original randomly generated pH. The frequency, duration, and amount of pH decrease were determined following the examination of daily pH values from Shaver's Fork, West Virginia (Dunshie 1979). From those data, we detected nine events in two 3-mo periods with mean decrease and recovery time calculated using the procedure just described. Most of these pH depressions were correlated with large rainfall events. These patterns agree with similar major precipitation events described in Harvey and Whelpdale (1986).

The model simulated 365 d using data of each of the three species and used the following sequence of calculations. On day one, a random run-length and a random pH were selected from the appropriate random distributions described above. For each such pH value, the appropriate cumulative survivorship was calculated from the fitted Weibull distribution for the species using the 24-h exposure curve. For each subsequent day during that run, a new cumulative survivorship was calculated using the appropriate exposure curve (i.e. 24, 48, 72, 96 h). Thus, a series of cumulative survivorships were calculated to estimate survival at that pH for exposure times ranging from $t=1$ to $t=$ runlength. Survival at exposure times exceeding 96 h were linearly extrapolated from the 72- and 96-h shape and scale parameters for *Gammarus* and *Isoperla* or interpolated from the 96-h and 43-d shape and scale parameters for *Pteronarcella* (Gaufin 1973). Once these cumulative survival rates were known, the daily rates were computed as the ratios of successive cumulative values. The daily rates were saved for later statistical processing. For example, if the run-length was 3 d and random pH 5.5, then we examined the Weibull fits of empirical data for the survivorships at that pH for the 24-, 48-, and 76-h experiments. If these cumulative survivorships were 0.4, 0.2, and 0.2, respectively, then the daily rates would be 0.4, 0.5, and 1.0 for $t+1$, $t+2$, $t+3$ for that 3-d period of constant 5.5 pH. This sequence of calculations was repeated until time equalled or exceeded 365 d by obtaining a new run-length value from the appropriate distribution and incrementing the current simulation time by run-length days.

Statistical Analysis

As described below, we used analysis of variance and visual inspection of graphs to assess effects. The dependent variable used to compare the null model with data was the mean daily survival rate. Since we wished the null model to extend beyond the typical 96 h, cumulative survivorship was inappropriate as it depends on the duration of the experiment or simulation. Using the mean of the daily survival rates as the dependent variable precludes the use of chronic data for *Pteronarcella* (43 d exposure) because the means of daily survival rates could not be calculated for this exposure period. Daily survival rate (the ratio of successive values of cumulative survivorship) varies over the course of an exposure experiment, and, thus, there is no unique value against which to compare the model. Moreover, it does not incorporate survivorship on previous days. For example, if day 1 and day 2 each had a cumulative survivorship of 0.3, the daily survival rates would be 0.3 and 1.0. Use of this measure in a statistical analysis will bias the results due to the artifact of computing daily survival rates from cumulative rates.

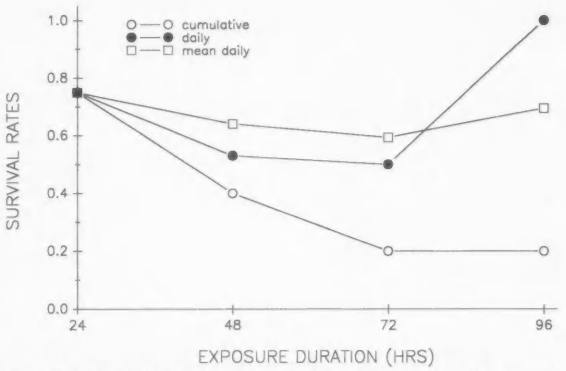

FIG. 3. Relationship between cumulative survivorship, daily survivorship, and "mean daily survivorship" for *Gammarus lacustris* at pH 5. Data from Gaufin (1973); see text for details.

Mean daily survival rate has none of these deficiencies. We define it as the arithmetic average computed over the unit of time appropriate to either the model or the data. Mean daily survivorship is based on the time trajectories of cumulative survival rates for a fixed pH. By calculating successive ratios over time of these trajectories, daily survival rates are computed. Mean daily survival rates for an experiment of duration of m days or model run-length of m days are computed for each time period less than or equal to m, i.e. $m-1$, $m-2$, $m-3$, etc. For example, Fig. 3 shows the time trajectory of cumulative survival rate for a species in our data set in a 4-d experiment at pH 5. Also plotted is the daily rate calculated as successive ratios. Mean daily rate at time 4 is the average of the four daily rates from day 1 (24 h) to day 4 (96 h) as plotted. Mean daily rate at time 3 is the average of the three preceeding daily rates. In general, the mean daily rate at time j is

$$(4)\quad MDS_j = \frac{\sum_{i=1}^{j} DS_i}{j}$$

for the jth mean daily survival rate (*MDS*) using the previous i daily survival rates (*DS*). With these sets of numbers, we can compare the differences between the model and each of the experiments of duration j days.

To explore the usefulness of the null model to extrapolate from one mean pH value to another, we regressed, for each species separately, the responses at higher mean pH on to the responses at lower pHs. For example, pooling all treatment results, we regressed mean daily survival rates at pH 6 against those at pH 4. We also regressed the responses at pH 6 against pH 5 responses, and pH 5 responses against responses at pH 4.

We also performed probit analysis using the Statistical Package for the Social Sciences (SPSS 1983) based on the mean of the mean daily survivorship values for each treatment to estimate LC-50. Only those simulated treatments which differed in the pH level (pH 4, 5, 6) were combined for each probit analysis.

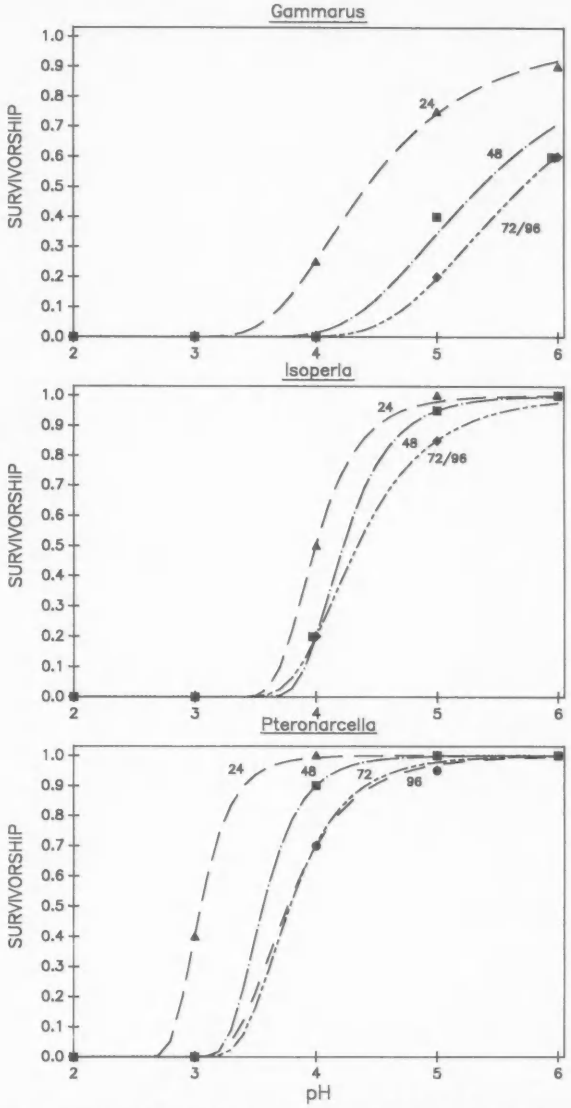

FIG. 4. Observed data and curves using best fit parameters to a modified Weibull survival function for *Gammarus lacustris*, *Isoperla fulva*, and *Pteronarcella badia*. Data from Gaufin (1973).

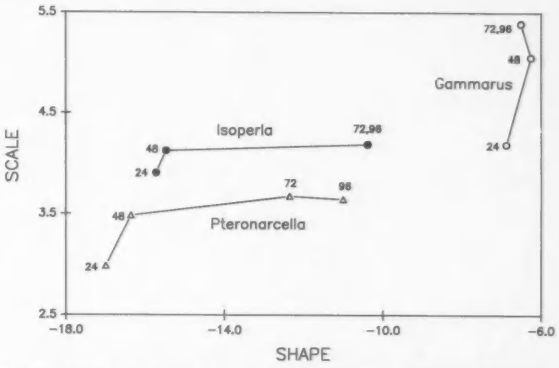

FIG. 5. Location of three macro-invertebrates in the parameter space of a modified Weibull survival function. Numbers are the laboratory exposure durations in hours from which the parameter estimates were made. Scale = parameter '*b*' and shape = parameter '*c*' in equation (3).

Three methodological issues arise in this analysis. First, LC-50s depend on the duration of exposure to the stress, but our simulation model produces mean daily survivorship. Using the mean of the mean daily survival rates for each of the Monte Carlo pH values (i.e. 4, 5, 6) for probit analysis is equivalent to the empirically based probit analysis for test durations of 24 h. The second methodological problem concerns the number of organisms to be used in the probit analysis of Gaufin's (1973) data and simulation model output. LC-50s are insensitive to the sample size, but confidence intervals are not (Robertson et al. 1984; Smith et al. 1984). Gaufin (1973) did not report initial animal numbers in his tests, and our model produces only survivorship. For the purposes of these comparisons, we assumed 100 animals as the starting conditions for both our recalculations of the LC-50s of Gaufin's (1973) data and our model output. This number is approximately that which produced the smallest confidence intervals of all sample sizes examined by Robertson et al. (1984). Finally, SPSS probit analysis requires at least four values for the independent variable. As our studies varied only three pH values, we supplemented our model results with Gaufin's (1973) results for pH 2 and 3. As required for meaningful probit analysis, all analyses reported contained at least three data points that were neither 0.0 or 1.0. Since this is a relatively small number of points, the power of tests based on these analyses will be limited.

Results

The Weibull parameter estimates at each exposure duration for the three species examined in detail below are shown in Fig. 4. The earlier classification of the species as "resistant," "intermediate," and "sensitive" is evident from this figure. The relationship of the species and the effects of test duration on the shape of the curves in Fig. 4 is shown in Fig. 5. This plots the location in parameter space of each test. Note that the stoneflies (*Pteronarcella* and *Isoperla*) have similar parameters and these differ from the amphipod (*Gammarus*). Further, within each species, the values appear to converge as the duration of exposure increases, but the stoneflies, unlike the amphipod, show a large change in response when exposed for 3 versus 2 d. The scale parameter is relatively independent of exposure duration in *Isoperla* and *Pteronarcella*, while the shape parameter is relatively independent of exposure duration in *Gammarus*.

To determine if any laboratory exposure data could accurately be extrapolated to random environments, we made 1296 comparisons (108 treatments × three species × four laboratory values). By a two-tailed *t*-test, the laboratory data were significantly different ($P<0.05$) from the simulated survivorships for all but three of the 432 treatments for *Gammarus*, two of the treatments for *Isoperla*, and two of those for *Pteronarcella*. In other words, had the dose–response experiments been performed as described in our simulations and had the organisms responded in a quantitatively similar manner to their response in constant conditions, then we expect agreement between con-

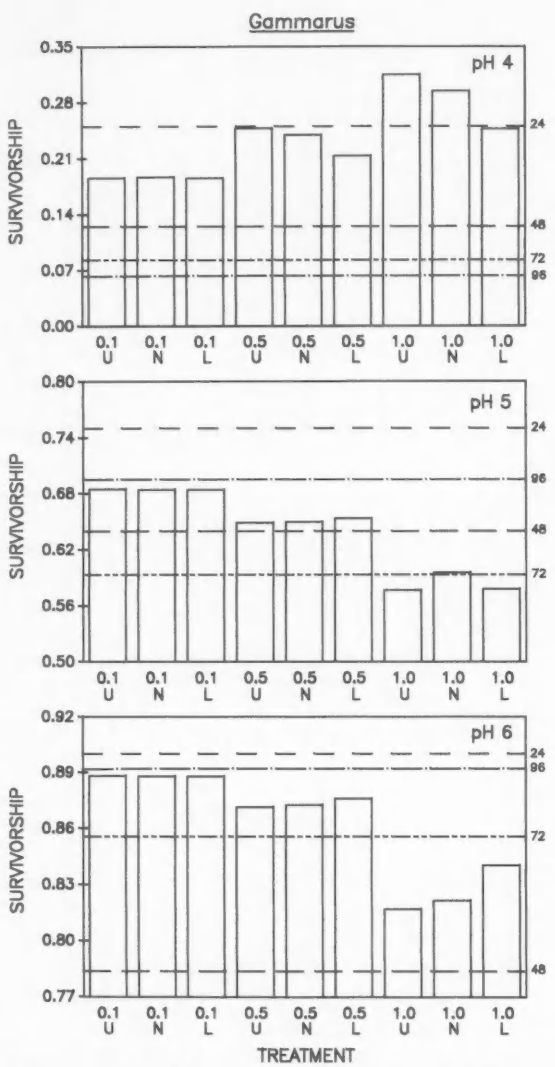

FIG. 6. Simulated mean daily survival rates for *Gammarus lacustris* for nine treatments and three mean pH levels. Each treatment is a combination of standard deviation (0.1, 0.5, or 1.0) and distribution [uniform (U), normal (N), or log-normal (L)] of pH values. Horizontal lines are the mean daily survivorships from laboratory data of different exposure durations as identified by the numbers on extreme right.

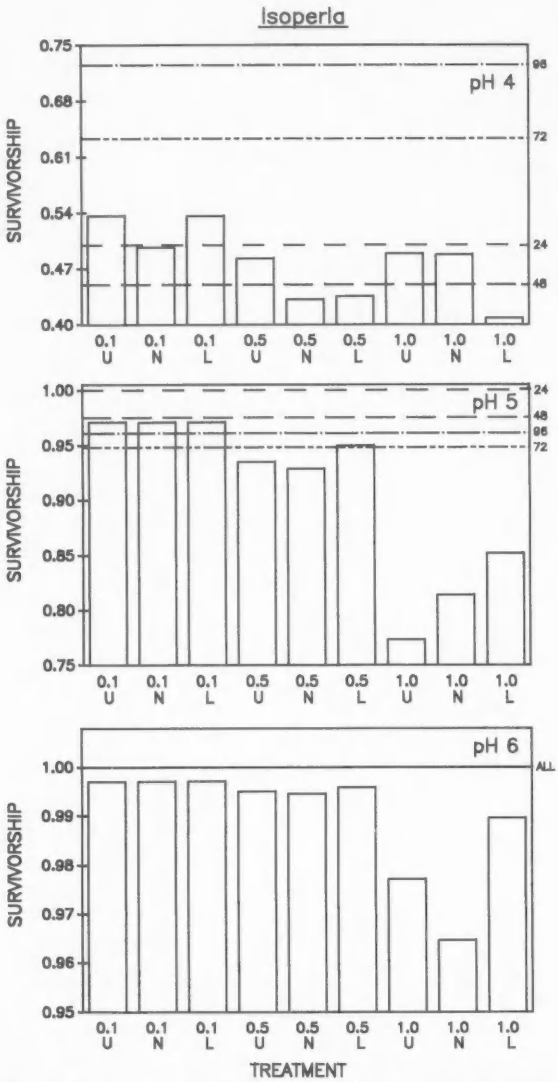

FIG. 7. Simulated mean daily survival rates for *Isoperla fulva* for nine treatments and three mean pH levels. Treatment identifications as in Fig. 6.

stant and variable environments in only 0.5% of possible combinations of the tested characteristics of disturbances.

Species Comparisons

Figures 6–8 indicate the magnitude of the extrapolation errors for a subset of these comparisons. The simulated and observed mean daily survival rates for each species after removing the results for the fixed (nonempirical) run-length distribution and episodic events treatments are shown. Unless otherwise noted, error bars on simulated results are too small to plot and experimental data are significantly different.

Gammarus (Fig. 6) shows great variability in both the simulations and the experimental data. At pH 4, increasing variability increases survivorship (compare 0.1/normal and 1.0/normal), but this is reversed at higher pH levels. At pH 5 and 6, short dose–response experiments (24 h) overestimate survivorship in random environments. This is most severe with large variability in pH. At low to intermediate levels of variability, laboratory data underestimate *Gammarus* survivorship. Distribution type has little effect, except at standard deviation 1.0. No single laboratory exposure period is uniformly a good predictor of response given the variable conditions we examined, but for the treatments shown here, at pH 4, 24-h tests do best and at pH 6, 72-h tests do best, overall. The responses at 0.5/uniform and 1.0/log-normal are not statistically different than

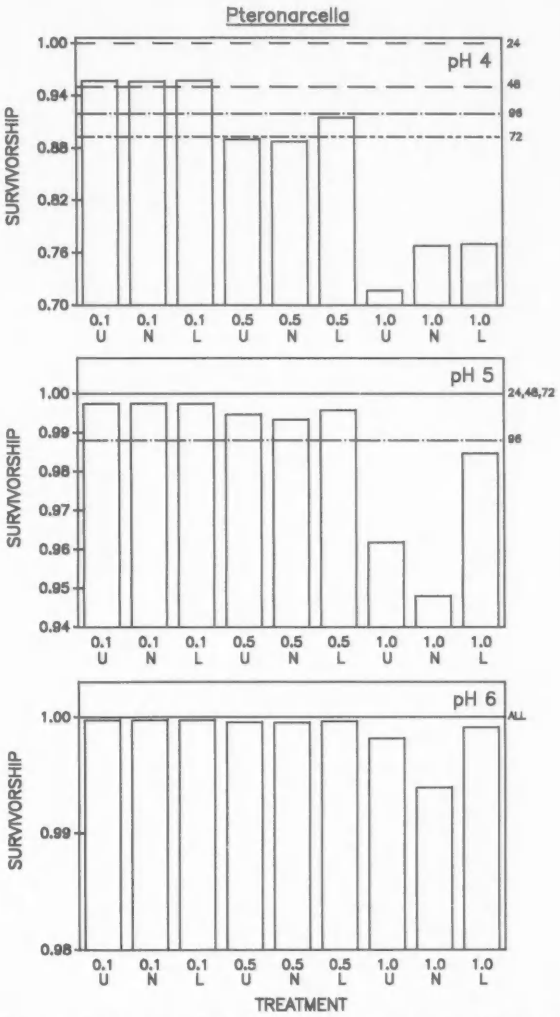

FIG. 8. Simulated mean daily survival rates for *Pteronarcella badia* for nine treatments and three mean pH levels. Treatment identifications as in Fig. 6.

the 24-h exposure experiments. At an intermediate pH of 5, the 96-, 48-, and 72-h tests all do relatively well, depending on the level of variability. The response at 1.0/normal is not statistically different than that observed for 72-h durations. Response at pH 6 is similar to that at pH 5, but survivorship levels are higher.

Isoperla has, in general, an intermediate response to pH (Fig. 4) and, as a result, its response to our treatments is also variable (Fig. 7). The response at 0.1/normal at pH 4 is not different from the 24-h experiments; the treatment at 0.5/log-normal at pH 5 is not different than 72-h experiments. At pH 4, response varied with the statistical distribution from which pH values were drawn. At higher pH, this became less important, except at large standard deviations. Variability, in general, decreased survivorship; the largest proportional decrease (0.25) occurred at pH 4 using a log-normal distribution between standard deviation 0.1 and standard deviation 1.0. At pH 4, long duration experiments (96-h) predict mean daily survivorship poorly, 24-h and 48-h durations are closer, but all are significantly different than expected from our simulations. At higher pH values, increasing variability increases the difference between laboratory and simulated results. At pH 6, the constant laboratory conditions of all durations tested indicated no mortality, but our simulations predict mortality of 0.5–3.5%, depending on type and standard deviation of the distribution.

As a resistant species, the response of *Pteronarcella* (Fig. 8) is generally opposite to that of *Gammarus*. Increasing variability is detrimental to all pH values. Comparing all pH levels, the greatest relative decrease due to random variability occurred at pH 4 using a uniform distribution between standard deviations 0.1 and 1.0. The only effects of distribution occurred at standard deviation 1.0; at the other levels of variability, the type of distribution had little effect. Since pH has little effect on *Pteronarcella*, the observed data approximate the expected survivorship in variable environments. Long duration experiments (72 and 96 h) tend to underestimate the survivorship expected in environments with standard deviation 0.1. At pH 6, all laboratory estimates of survival are 1.0 and above the simulated values.

To examine treatment interaction, 12 5-way ANOVAs of all 108 treatments for each species were performed using the differences between the observed mean daily survivorship of each length of laboratory test and the mean daily simulated survivorships. Each 5-way factorial ANOVA tested 31 unique combinations of main effects and interactions. The overall F-value for each ANOVA was significant. For 359 of 372 tests, the treatments (main effects) and interactions were significant ($P<0.01$). The number of treatments which did not produce significant results (13) are within the range expected by the type II error at this significance level. The data were not normally distributed, and this may have affected the ANOVA result, but this would have biased the test to refuse to reject the null hypothesis rather than reject it.

Standard Deviation

Thirteen of 372 tests of the effects of standard deviation on survivorship were not statistically significant. Of these, 10 were associated with *Pteronarcella*, the resistant species. The effects of increasing standard deviation of pH fluctuations from the normal distribution are shown in Figs. 6–8 by comparing treatments 2, 5, and 8 at each pH. Similar patterns are present for uniform and log-normal distributions. At pH 4, *Gammarus* (Fig. 6) shows a significant increase in mean daily survivorship as standard deviation increases from 0.1 to 1.0. This effect is reversed for pH 5 and 6. The relatively resistant species (*Pteronarcella*) shows a dramatic decrease in survival rate as standard deviation increased at pH 4. This is ameliorated at higher mean pH levels, due to high survivorship in the laboratory tests at these pH values (Fig. 4). *Isoperla*'s response to increasing environmental fluctuations at pH 4 is complex (Fig. 7), showing a decrease followed by an increase in mean daily survivorship. The overall trend, however, is consistent with pH 5 and 6; increasing variability decreases survivorship.

Distribution

The effect of different statistical distributions of pH levels varied between species, standard deviation, and mean pH values such that no overall trends were observed. *Pteronarcella* was more sensitive to the normal distribution at standard devia-

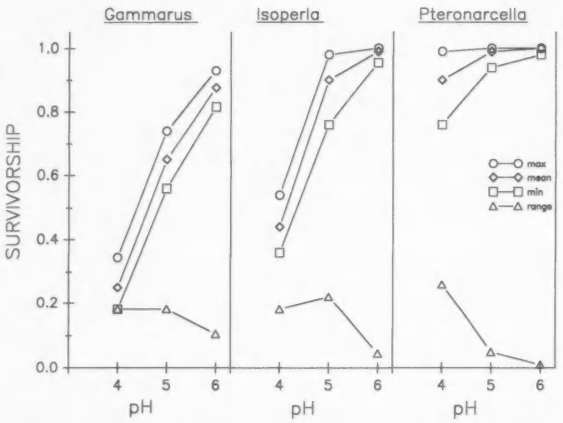

FIG. 9. Summary of responses of the three species to all simulated treatments. The maximum, minimum, and mean of the mean daily survivorships are shown for each mean pH treatment. The range is the difference of the maximum and minimum.

tion of 1.0 (highest) at all pH values and to both the normal and uniform distributions at low mean pH and a standard deviation of 1.0 (Fig. 8). At the lowest pH value, the normal and uniform distribution treatments exhibited lower survivorships. Treatments at higher pH values and lower standard deviations did not show an effect due to the different distributions.

Gammarus at pH 4 generally was affected by the distribution at the two higher standard deviations (Fig. 6). The log-normal distribution produced the lowest mean daily survivorships with the normal distribution also producing low survival. This trend was repeated at pH 5 for the two lowest standard deviations, but at standard deviation 1.0, the trend was reversed with uniform distribution treatments producing the lowest survivorships and log-normal treatments exhibiting the highest. At pH 6, the effect due to different distributions was not apparent.

At pH 4, *Isoperla* showed an effect due to distribution at all standard deviations (Fig. 7). The importance of this effect was diminished as pH increased. At pH 6, *Isoperla* responded like *Pteronarcella*; at standard deviation 1.0, distribution had an effect, with the log-normal producing the lowest survivorship.

For all species, at standard deviation 1.0, the uniform distribution produces lowest survivorship at pH 4 for *Pteronarcella* at pH 5 for *Isoperla*, and at pH 6 for *Gammarus*. Figure 4 indicates that these pH values for each species occurs near the "shoulder" of the Weibull survival curve. This pattern holds for other comparisons (e.g. the effect of standard deviation) across these three pH values and species. Further support for the generalization that the interaction of mean pH and the relative position of the Weibull survival curve (Fig. 4) determines responses is present in the comparison of all nine histograms for *Isoperla* at pH 6 (Fig. 7) and those for *Pteronarcella* at pH 5(Fig. 8).

Mean pH

Figure 9 summarizes the mean responses of all these treatments by showing the range and average survivorship for each of the mean pH values used after pooling the mean of 100 replicates of all treatments. Inferential statistical analysis is inappropriate here since the descriptive statistics shown are based on the pooled means of 35 treatments. Reducing only the mean

TABLE 1. Regression r^2 for predicting responses at one pH from responses at another.

	pH 4 versus pH 5	pH 5 versus pH 6	pH 4 versus pH 6
Gammarus lacustris	0.182	0.925	0.213
Isoperla fulva	0.027	0.739	0.002
Pteronarcella badia	0.641	0.827	0.341

pH value within a set of treatments resulted in lowered mean daily survivorship values. *Gammarus*, the sensitive species, experienced the greatest reduction in survivorship (from 88% survival at pH 6 to 25% survival at pH 4 averaged over all treatments). *Gammarus* also showed the lowest survivorship within each pH treatment (18% at pH 4, 56% at pH 5, and 82% at pH 6). *Pteronarcella* had both the highest survivorship at any pH (100% at pH 4, 5, and 6) and the least amount of reduction in survivorship. Averaged over all treatments, *Pteronarcella* showed a reduction in survivorship with pH. *Isoperla* displayed an intermediate response with a large reduction in survivorship at low pH values and a much smaller reduction at high pH values (38, 76, and 96.5% at pH 4, 5, and 6, respectively).

Run Length

Although not documented here, response to the two run-length distributions was dependent upon the mean pH and the statistical distribution from which the run-length random deviates were drawn (Fig. 2). Generally, survivorship was reduced in the empirical run-length distribution over that of the uniform run-length distribution with a mean of 1.0. This may be due to the increased number of pH events with duration longer than 1 d. The greatest reduction in survivorship occurred after 2–3 d. Longer run-lengths produced a gradual decline in survivorship to day 3 or 4. Mean daily survivorship of *Isoperla* and *Gammarus* increased in subsequent days, as no further reduction in numbers occurred. An exception to this general trend was *Isoperla* at pH 4 and standard deviation 0.1 in which the empirical run-length treatments had greater survivorship over that of the fixed run-length distribution.

Episodic Events

Episodic events produced varying effects depending on the species, distribution, standard deviation, and run-length distribution. Generally, treatments with episodic events displayed decreased survivorship or had no biological effect. Only in *Isoperla* at pH 4 and standard deviation 0.1 did treatments with episodic events consistently have higher survivorships regardless of distribution and run-length.

Interactions

Interactions between the factors produced unpredicted results. Empirical run-lengths, and high standard deviations produce the lowest survivorship for *Gammarus* at pH 5 and 6, but are among the highest at pH 4 (Fig. 6). These two factors with a pH level account for most of the variation in the survivorships of *Gammarus*.

With *Isoperla*, standard deviation and statistical distribution have the greatest effect upon survivorship at all pH levels. Based on regression r^2 (Table 1), high survivorship at pH 4 was a poor predictor of high survivorship in the same treatment at pH 5 or

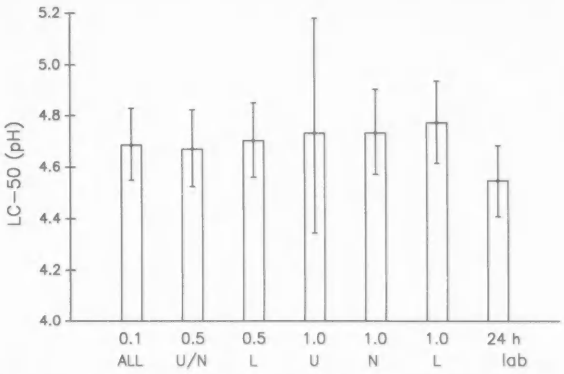

FIG. 10. LC-50s and confidence intervals based on simulated and observed data for *Gammarus lacustris*. Treatments are combinations of standard deviation and distribution as indicated, where U = uniform, N = normal, L = log-normal.

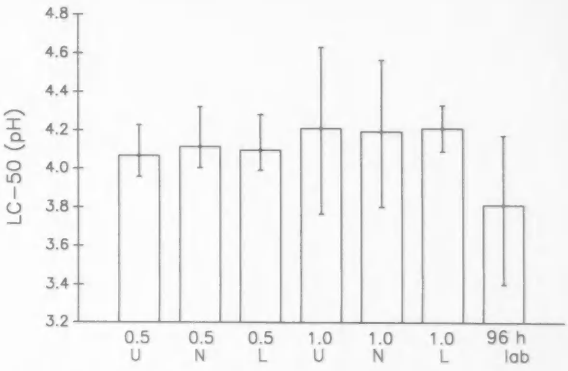

FIG. 11. LC-50s and confidence intervals based on simulated and observed data for *Isoperla fluva*. Treatment identifications as in Fig. 10.

6. Treatments at pH 5, however, were good predictors of survival at pH 6. These patterns were true for all species.

Pteronarcella experienced lower survivorships at higher standard deviations at all pH values. Effects of other factors (statistical distribution, episodic events, and run-length) were also more pronounced in treatments with high standard deviations.

Probit Analyses

Probit analysis (Figs. 10 and 11) produced large confidence intervals about the LC-50s of the observed data. There is no statistical difference between the LC-50s for different exposure durations, even though there is wide separation in the Weibull parameters (Fig. 5). Moreover, comparison of the empirical LC-50s for 24-h exposure tests with those of the "24-h" simulated data shows no significant difference. This is contrary to other measures of population response (e.g. survival rate) as discussed above (Figs. 6–8).

Discussion

Major Trends

Although the results were complex, several major patterns stood out. Most noticeable was the obvious differences between the mean daily survival rate in constant laboratory conditions and those predicted by our null simulation model. In all but a few cases, the observed values were significantly different from those produced by Monte Carlo simulation. Many cases showed dramatic differences between observed and predicted. Even small differences in daily survivorships are translated, over time, to large cumulative survivorship differences. The extent of disagreement depended on the measure of response used. Daily survivorship showed great differences, but LC-50s showed smaller or no differences. This is discussed below.

Two manipulated variables that had substantial effects were the mean pH and the standard deviation of the distribution of random pH values. Mean pH effects were clear as comparisons of the different pH responses of Fig. 4 for each species indicate. Two major patterns emerged from comparing the effect of standard deviation on mean daily survivorship. First, for low mean pH and sensitive species, increasing variance of the stressing environment increased survivorship. This effect is related to Levins' (1979) and Armstrong and McGehee's (1980) concept of "exploiting variance" in a competitive network. It exemplifies the adage true of nonlinear relationships: "the mean of the response does not equal the response at the mean." While this is obvious from Fig. 1, neither its quantitative magnitude nor its ecological significance are clear without the assistance of a model. Secondly, at high mean pH (when the response at the mean pH is on the "shoulder" of the Weibull survival curve), increasing variance decreases survivorship. Thus, there is a strong interaction between the shape of the survival curve and the mean and standard deviation of pH fluctuations in the environment.

The nature of the distribution from which random deviates were drawn did not have a major effect on the output of the null model. The situation under which these effects may be noticeable depend on a balance of the nature of the population (resistant or sensitive) and the mean and standard deviation of the environment. These conditions occurred in *Isoperla*, a species of intermediate sensitivity. Between pH 4 and 5 its response is approximately linear and symmetric about its response at the mean pH. An asymmetric random distribution of the environment, such as the log-normal, produces an asymmetric response. This, then, has the potential of interacting with other variables (e.g. standard deviation) to mimic the effects observed with symmetric distributions as they influence species (e.g. *Pteronarcella* or *Gammarus*) with nonlinear responses near the mean pH.

We also demonstrated the importance of the characteristics of the run-length distribution. This could be as important as mean pH, since it determines the length of time organisms are exposed; the importance of these effects in laboratory tests are well documented and obvious from Fig. 4. Based on comparisons of an empirical distribution and one with uniform durations of 24 h, they also play an important role when environments are random.

There is currently great interest in the potential importance of episodic events on survival rates of organisms subjected to low pH environments (e.g. Harvey and Whelpdale 1986; France and LaZerte 1987). Typically, these events are thought to be annual, short-lived, rapid decreases in pH. They are usually correlated with meterological events such as spring snowmelt

or major rainstorms periods (Harvey and Whelpdale 1986). We implemented episodic events in our simulations as more frequent and less intense than most authors, due to the correlations of the events used here with rainstorms. With some exceptions, we found little effect of episodic events on survivorship. These results may be due to our implementation of the phenonmenon.

Ecological Significance

To evaluate fully the relevance of this null model, one must understand the ecological significance of the quantitative differences between laboratory and model mean daily survival rates. The potential importance of these differences, in a linear model of population growth, is quite large, but ecological relationships are typically nonlinear and small parameter differences are not always translated into large population differences. These results need to be embedded in an ecosystem model either directly (e.g. O'Neill et al. 1982) or as the basis for a sensitivity analysis (Swartzman and Kaluzny 1987) in order to properly evaluate their significance. An aspect especially interesting to explore would be the community effects of competing species' responses to the variance of the stress. For now, there is inadequate field data for the organisms we studied to determine if temporal variability has the effects on survivorship that our model experiments suggest.

Model Extrapolation

We are unable to investigate the extent to which our null model can be extrapolated to other environments with more variable run-length distributions, different mean pH levels, other statistical distributions, and so on. We purposefully chose, however, variables for study that characterize the major features of disturbances (Pickett and White 1985). Moreover, the values of the variables that we examined represented the extremes (e.g. 0 and 36 episodic events per year) relevant to the particular organisms and empirical data sets we had available. If coupled with explicit laboratory tests of the results, additional Monte Carlo simulations could be informative.

Recently, France and LaZerte (1987) described results of a model similar in scope to ours. Using relatively longer laboratory exposure durations, they estimated mortality curves as a function of pH in *Hyalella azteca*. From these and an analysis of duration of pH values during low pH snowmelt events, they estimated mortality and population size. Although their model and ours use different methods for calculating expected survival rates, the objectives are similar: extrapolate laboratory dose–response data to fluctuating environments. We have focused on the effects of different characteristics of typical daily pH fluctuations. France and LaZerte (1987) emphasized a specific, empirical episodic event during spring snowmelt. Although the following comparison is rough, it suggests that the conclusions of the two models are similar.

After converting some data of France and Stokes (1987, their figure 1) to our format (e.g. Fig. 4), it appears that *H. azteca* is similar to *Isoperla* (Fig. 4). Both species showed a rapid increase in survivorship between pH 4 and 5 for exposure durations of 48 and 96 h. Further, by graphically estimating times and pH values during snowmelt at site 14 (France and LaZerte 1987, their figure 4), we estimated that over the 46 d of the event mean pH was 4.7 and the standard deviation was 0.2. The time–mortality response of *H. azteca* (France and LaZerte 1987, their figure 3) indicates that expected cumulative mortality for constant pH 4.7 for 46 d would be >95% (probably >99%). Using their model, they estimated cumulative mortality to be 77.2%. Thus, the nonlinearity of the time–mortality surface for *H. azteca* causes higher survivorship than expected from constant laboratory conditions. Although our simulations do not correspond exactly to pH 4.7 and standard deviation 0.2, the closest case (Fig. 7, pH 5, normal distribution, standard deviation 0.1) had a mean survivorship of approximately 0.97. This is higher than laboratory exposures of 72 and 96 h, but less than those for 24 and 48 h. Applying our method of calculating mean daily survivorship to the time trajectory of cumulative survivorship of France and LaZerte (1987, their figure 4), we obtained a mean daily survival rate of 0.98. Thus, it may be that the relatively short event presented by France and LaZerte (1987) is acting like a normal distribution with mean pH of 4.7 and standard deviation of 0.2. In any case, there appears to be a convergence between two different, independent models, indicating that the general conclusions reached are robust.

Recommendations

Our results indicate that extrapolation of laboratory results obtained under constant conditions to variable environments will be difficult, if the daily rate of survival is of interest. We observed fewer differences when LC-50s are used, but for reasons cited above, we question the utility of these measures. For survival rates, all of the commonly used exposure durations (24, 48, 72, and 96 h) were inadequate predictors under one or more conditions of environmental variability. No duration was consistently closest to the expectations of our model. In particular, longer durations (e.g. 96 h) did not predict better than short durations. Nor was there consistency to the bias that results from using 96-h tests as the basis for extrapolation. Under some conditions, laboratory data overestimated survival rates, for others they underestimated survivorship. Were the survival rates used to set environmental regulations, as LC-50s currently are, the laboratory data could be either too liberal or too conservative, relative to those made using LC-50s.

While we respect the uses of reporting the results of dose–response experiments as LC-50s, we agree with Borgmann et al. (1978) that this index has limited use. We suggest that investigators also report either the raw numbers surviving or, preferrably, parameter values and their variances for the fit of the data to useful functional forms such as the Weibull distribution. It is crucial that the numbers of animals used in these tests be reported, as well as confidence intervals. Further, we recommend that temporal variability be incorporated into laboratory dose–response experiments directly. This may best be done using a factorial design as we have attempted with computer simulation and experimentally by Thorp and Wineriter (1981) for temperature stresses. Such practises will not only provide data to test certain aspects of disturbance theory (Pickett and White 1985), they will improve the basis for extrapolating these data to natural systems. Moreover, much insight and an increase in statistical rigor can be obtained by using null models of the type described here with data produced in variable environments. All these suggestions imply more work and cost for toxicity studies, but we feel that this cost out-weighs the risk of bias and error in socially important management decisions.

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Size Distribution of the Macroinvertebrate Community in a Freshwater Lake[1]

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Macroinvertebrates were collected every 2 wk for 18 wk from three depth zones in a deep lake in Alberta. Unionid clams comprised 80% of the total macroinvertebrate biomass and were excluded from initial analyses. The seasonal average size-spectrum for the littoral zone community was bimodal with peaks in the 8–16 and 256–512 mg weight-classes; size-spectra for the sublittoral and profundal communities were unimodal with peaks in the 8–16 and 16–32 mg weight-classes, respectively. Slopes of the normalized size-spectra for the littoral, sublittoral, profundal, and whole-lake communities were not significantly different from −1.0, −1.0, 0.0, and −1.0, respectively. These results suggest that biomass is evenly distributed across logarithmically even size-classes for the average macroinvertebrate community in the littoral zone, sublittoral zone, and on a whole-lake basis. The biomass peak for unionids (16.4–32.8 g weight-class) was 10–30 times greater than biomass peaks for the remaining macroinvertebrates. The slopes of normalized size-spectra for the littoral zone and whole-lake were changed significantly when unionids were included; however, unionids presumably play a minor role in the macroinvertebrate community because they are an energy sink in the present context. Despite wide seasonal variation, average normalized size-spectra based on samples collected at 4- and 6-wk intervals were very similar to those based on nine biweekly collections.

Des macro-invertébrés ont été ramassés à toutes les 2 sem durant 18 sem à trois profondeurs différentes dans un lac profond de l'Alberta. Les Lamellibranches de la famille des unionidés constituaient 80 % de la biomasse totale des macro-invertébrés et nous les avons exclus de nos premières analyses. La distribution saisonnière moyenne selon la taille était bimodale dans le cas de la communauté littorale et les maximums correspondaient aux classes de 8–16 et 256–512 mg tandis que dans le cas des communautés sublittorales et de la zone profonde, les distributions étaient unimodales et les maximums correspondaient aux classes de 8–16 et 16–32 mg respectivement. Les pentes des distributions normalisées pour les communautés littorales, sublittorales, de la zone profonde et du lac pris dans son ensemble n'étaient pas différentes de −1,0, −1,0, 0,0 et −1,0 respectivement. Ces résultats semblent indiquer que la biomasse est répartie uniformément à travers les différentes classes, égales en terme logarithmique suivant les moyennes saisonnières, dans la communauté des invertébrés des zones littorales et sublittorales de même que pour le lac pris dans son ensemble. Le maximum de la courbe de biomasse des unionidés (classe de 16,4–32,8 g) était 10 à 30 fois supérieur à celui de l'ensemble des autres macro-invertébrés. Si l'on tient compte des unionidés, les pentes des distributions normalisées suivant la taille relative à la zone littorale et à l'ensemble du lac sont significativement modifiées; cependant, le rôle des unionidés dans la communauté des macro-invertébrés est présumément peu important parce que ces mollusques ont un régime alimentaire différent de cleui de la plupart des autres macro-invertébrés et sont passablement à l'abri des prédateurs. Malgré les variations saisonnières importantes, les courbes de distribution moyenne normalisés établies à partir des échantillons ramassés à des intervalles de 4 et 6 sem étaient très semblables à celles établies à partir d'échantillons ramassés aux 2 sem à neuf reprises.

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Particle size-distributions increasingly are being used to evaluate the structure of aquatic ecosystems. In the marine pelagic zone, the biomass of organisms is roughly equal across logarithmically increasing size-classes (Sheldon et al. 1972; Sheldon et al. 1977; Rodriguez and Mullin 1986) and a general theory has been developed to explain this pattern (Kerr 1974; Sheldon et al. 1977; Silvert and Platt 1978). Peters (1983) found a similar pattern in the planktonic community of a freshwater lake. However, other workers have described characteristic peaks and troughs in the size distributions of the planktonic community of lakes (Sprules et al. 1983; Sprules and Munawar 1986). These models can be used to predict the biomass (Sheldon et al. 1977; Borgmann 1982) or production (Borgmann 1982, 1987; Minns et al. 1987) for any size-class if the biomass or characteristic turnover rate, respectively, in another size-class is known. In addition, Kerr (1977) and Sprules and Munawar (1986) suggest that among-lake differences in the size-distributions of pelagic organisms can be attributed to differences in productivity or perturbation among the lakes. However, Sprules and Munawar (1986) also point out that, for freshwater lakes, there is little information on the benthic community, the littoral zone, or on seasonal variation in size-distributions in any size-class.

Although the littoral zone supports the greatest biomass and productivity of macroinvertebrates (Efford 1969; Kajak and

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Dusoges 1975; Jonasson 1978; Sarvala et al. 1981) and lentic fishes obtain most of their energy from the benthos (Eggers et al. 1978; Wissmar and Wetzel 1978; Boisclair and Leggett 1985; McQueen et al. 1986), there is relatively little information on the links between benthic macroinvertebrates in lakes and other functional groups. Fish biomass and yield are strongly correlated with macroinvertebrate biomass or production (Matuszek 1978; Hanson and Leggett 1982), and recent field experiments support the hypothesis that the macroinvertebrate biomass in a given lake can only support a specific biomass of fish (Hanson and Leggett 1985, 1986). However, fish growth and, therefore, production depends on the availability of food of suitable size (Kerr 1971; Timmons et al. 1980; Diana 1987). Knowledge of the biomass size-spectra of macroinvertebrate communities would, therefore, provide vital information on trophic dynamics in lakes.

Recently, Mittelbach (1981) found that length-frequency distributions of invertebrates <20 mm long in bare marl sediments and on aquatic macrophytes in the littoral zone of a small lake are log-normally distributed. Consequently, weight-frequency distributions may also be log-normally distributed, and thus, macroinvertebrate communities should be amenable to useful description by means of biomass size-spectra. The few published studies on lentic invertebrate communities describe the size-distributions of very small organisms. Strayer (1986) looked for patterns in the size-distribution of the metazoan community (1 ng–1 mg, dry weight) collected from various depths in Mirror Lake. The biomass peak was in the largest size-class, 0.1–1.0 mg, (0.7–6.6 mg, wet weight). Cattaneo (1987) examined the size-distribution of invertebrates (4 μm–2 mm, equivalent spherical diameter) that colonized plastic "plants" in the littoral zone of Lake Memphremagog. Again, the biomass peak was in the largest size-class examined: 1–2 mm equivalent spherical diameter (0.5–4.2 mg, wet weight). There appears to be no comparable data for the large invertebrates (macroinvertebrates) in lakes.

The goal of this study was to quantify the size-distribution of the macroinvertebrate (>0.1 mg, wet weight) community in a small lake. We analysed the size-distributions for the littoral, sublittoral, and profundal zones separately because these zones differ substantially with regards to primary production, oxygen consumption, rates of sedimentation, and habitat complexity; factors that are known to affect the structure and abundance of benthic invertebrate communities. To our knowledge, this represents the first attempt to use biomass size-spectra and normalized size-spectra to describe freshwater macroinvertebrate communities.

Methods

Study Area

This study was done in Narrow Lake (54°35′N; 113°37′W), a small (1.14 km^2), deep (mean depth 14.2 m), moderately productive (mean summer total phosphorus 12.9 mg/m^3), and partially meromictic lake in central Alberta. Morphometry and water chemistry are described in Prepas and Trew (1983); Prepas and Vickery (1984); and Prepas and Trimbee (1988). The fish community consists of northern pike (*Esox lucius*), stunted yellow perch (*Perca flavescens*), burbot (*Lota lota*), Iowa darter (*Etheostoma exile*), and brook stickleback (*Culea inconstans*).

The littoral zone (depths from 0–6 m) represents 20.5% of the surface area of the lake. Four sampling stations were established in May 1986 (Fig. 1). The substrate at all four sites consisted of varied amounts of organic muck, decaying plant matter, and woody debris over fine sand. The macrophyte community was dominated by *Isoetes* and *Potamogeton filiformes* at site 1; young *Nuphar variegatum*, *Myriophyllum exalbescens*, *Chara*, and various species of *Potamogeton* at site 2; and *Chara* (<10 cm tall), *P filiformes*, young *Sparganium eurycarpum*, and an aquatic moss (*Drepanocladus* sp.) at site 3. Site 4 had a dense bed of *S. eurycarpum* to a depth of 0.5 m, an open area from 0.5 to 1.5 m, and a dense bed of *Chara* with patches of *Utricularia vulgaris* from 1.5 to 5.5 m. The *Chara* attained a height of 30–40 cm at the 2–3 m depth in August 1986 but was sparse from 4 to 5.5 m deep.

The sublittoral zone (depths from 6.1–15 m) represented 38.8% of the surface area of Narrow Lake. The four sublittoral zone sites sampled were continuous with the four littoral sites. The substrate at all four sites were predominately a brown organic muck with variable amounts of coarse sand and broken shells.

The profundal zone (depths from 15.1–38 m) represented 40.7% of the surface area of Narrow Lake. The two sites sampled were offshore from littoral sites 2 and 3 and represent the two deep holes in the lake. The sediments were composed of fine black organic mud, nearly all of which passed through a 500 μm sieve.

Collection of Macroinvertebrates

Macroinvertebrates (with the exception of unionid clams) were sampled with a 15 × 15 × 23 cm Ekman dredge fitted with a 500-μm screen on top. Collection of unionid clams is described later. We did not sample meiofauna, and crayfish are absent from Narrow Lake. We collected samples biweekly from 13 May to 2 September 1986 and used these data to examine seasonal variation in the size-spectra for macroinvertebrates in Narrow Lake.

On each collection date, we took samples from each depth zone. For each littoral site, three dredge samples were taken from each of the 1-, 3-, and 5-m depths. We only retained a sample if the dredge penetrated at least 10 cm into the substrate. In general, macrophytes are sparse and grow close to the substrate in Narrow Lake. Therefore, macrophytes did not hinder dredge operation and, when carefully taken, dredge samples collected both sediment and macrophyte-dwelling macroinvertebrates adequately. The only exception occurred in August 1986 when patches of *Chara* attained a height of 30–40 cm at the 3-m depth station at site 4. We did not try to avoid these taller patches and, therefore, some of the samples taken in August on this location were undoubtedly underestimates. We did not omit these samples because any one dredge sample only represents 1/36th of the littoral zone samples taken on a given date. A total of 324 samples were analysed from the littoral zone. At sublittoral sites 1, 2, and 3, three samples were collected from 7 m and four from 12–13 m. In addition, three samples were collected from 7 m at the fourth site to increase the sample size for the 7-m depth. A total of 216 samples were analysed from the sublittoral zone. Four samples were collected from each of 20–25 and 30–35 m depths at the two profundal zone sites. A total of 144 samples were analysed from the profundal zone.

All sediment samples were gently sieved through a 500-μm screen, preserved with 5% formalin (2% formaldehyde), and sorted by hand (within 10 d). Organisms were sorted to tax-

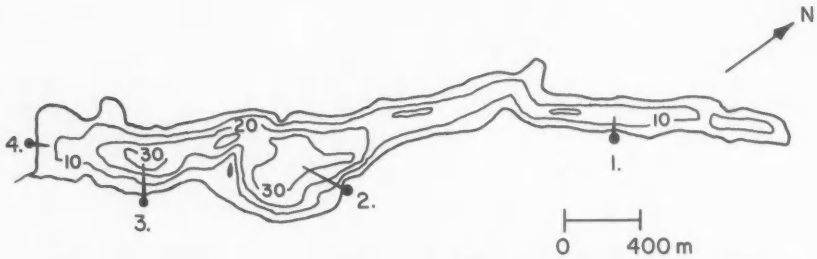

FIG. 1. Bathymetric map of Narrow Lake (contours in metres) showing the four collection sites.

onomic group (usually to family), enumerated, and stored in 5% formalin for 6–12 mo. Wet biomass of each taxon was determined to 0.1 mg and converted to fresh weight as described in Hanson and Leggett (1986). The geometric mean and 95% confidence limits (CL) of the total biomass were calculated for each depth zone and sample date as grams per square metre (fresh weight).

Sampling of Unionid Clams

Anodonta grandis simpsoniana is the only species of unionid clam in Narrow Lake. Unionid clams are found throughout the littoral zone with the exception of areas dominated by *Chara* >10 cm tall, about 20% of the littoral area (Hanson et al. 1988a). Clams were collected with a 23 × 23 × 23 cm Ekman dredge. Twelve sediment samples were collected at each of 1-, 3-, and 5-m depths for the 16 sites sampled from 28 May to 9 August 1986 and at each of 1-, 2-, 3-, 4-, and 5-m depths for the 19 sites sampled from 9 May to 19 August 1987. A total of 90 m^2 of sediment were sampled for clams. Details of sampling sites and sampler efficiency are described in Hanson et al. (1988a,b). All clams were taken, alive, to the laboratory where debris was removed and live weight and total length were recorded immediately. Throughout this paper live weight refers to the biomass of the living clam with the shell shut and includes the water inside the shell. The shell makes up about 15% of the live weight of *A. grandis simpsoniana* in Narrow Lake (Hanson et al. 1988a). The estimates of mean biomass and 95% CL were based on $\log_{10}$-transformed data.

Determination of Body Size

Body size is expressed as live weight (in milligrams) throughout this study. The biomass size-spectra were calculated separately for each depth zone and date. Whole lake-size spectra were calculated as the sum of area weighted size-spectra for the three depth zones. For each macroinvertebrate taxon, all individuals or a random subsample of 90–120 individuals (for sublittoral and profundal zones) or up to 220 individuals (for the littoral zone) were weighed to an accuracy of 0.01 mg. The preserved weights were corrected to live weight by multiplying by the appropriate correction factor. Size-frequency distributions were calculated at 1-mg intervals for each taxon, sample depth, and sampling date (as percent frequency). These individual frequency distributions were multiplied by the total number of organisms in that taxon, depth zone, sample date combination to yield the numerical size-frequency. The numerical size-frequencies for all taxa were then summed to give a total numerical size-distribution for each depth zone and sample date. These numerical frequencies were then expressed on a per square metre basis by multiplying by the appropriate correction factor (e.g. 36 samples represent 0.81 m^2 of sediment; the correction factor is 1.234). The numerical frequencies were converted to biomass size-frequencies by multiplying by the midpoint of each 1-mg size-interval. These distributions were then converted to percent frequencies and multiplied by the geometric mean total macroinvertebrate biomass for that depth zone and date which gave the biomass size-distribution on a per square metre basis.

Biomass size-spectra (Sheldon et al. 1972) were determined as the sum of biomass for $\log_2$-intervals beginning with 0–1 mg. Although we could weight organisms to an accuracy of 0.01 mg, we felt organisms <0.1 mg in biomass (mostly small oligochaetes and early instars of insects) were not adequately sampled. Therefore, we summed all organisms <1 mg in weight into one size-class.

Normalized size-spectra (Sprules and Munawar 1986) were determined by regressing $\log_2$ ((total weight in size-class)/(weight range in interval)) on $\log_2$ (upper limit of size interval) by least squares linear regression. The slope of these regression lines and the pattern of residual variation around the lines can be used to characterize the size-structure of the community and simplifies comparisons among ecosystems (Kerr 1974; Sheldon et al. 1977; Sprules and Munawar 1986). To date, this method has only been applied to pelagic communities.

Results and Discussion

The total biomass and biomass size-spectra for macroinvertebrate community (minus unionid clams) varied substantially among depths and dates (Fig. 2). The total biomass was higher in the littoral zone (overall mean 14.6 g/m^2) than in the sublittoral (overall mean 6.2 g/m^2) and profundal (overall mean 2.3 g/m^2) zones. In general, organisms >64 mg in weight (2^6 mg size-class) were only found in the littoral zone. The organisms >128 mg in weight (2^7 mg size-class) collected from the sublittoral zone from 10 June until 8 July represent two or three large leeches (*Nephelopsis obscura*) per sample date.

Biomass size-spectra varied widely among collection dates in all three depth zones (Fig. 2). In the littoral zone, there were biomass peaks in the 4–8 and 256–512 mg weight-classes in May, a single peak at 8–16 mg on 10 June, and no clear peaks from 22 July to 19 August. Organisms >128 mg in weight were absent from the littoral zone on 8 July but reappeared on 22 July. In early July there was a period of unusually heavy rain, including a 6-d period in which 147 mm of rain fell (Prepas and Trimbee 1988). Large areas of shoreline were already flooded on 8 July and this flooding had just begun to receed by 22 July. We think the sudden drop in total biomass from 14 g/m^2 on 24 June to 7.4 g/m^2 on 8 July, followed by an increase to 17.4 g/m^2 on 22 July, indicates many large orga-

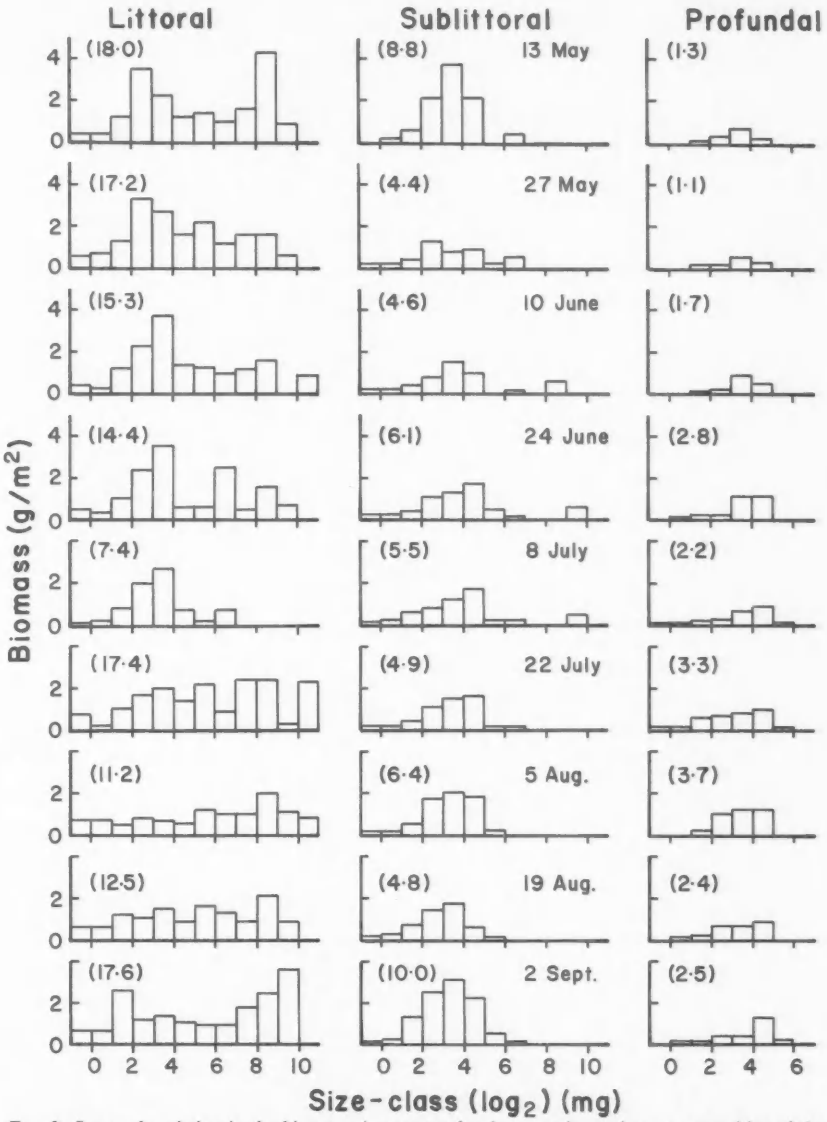

FIG. 2. Seasonal variation in the biomass size-spectra for the macroinvertebrate communities of the littoral, sublittoral, and profundal zones of Narrow Lake during 1986. Total biomass (g/m^2, wet weight) is shown in parentheses in each panel. Size-classes are in milligrams, wet weight.

nisms left the areas we sampled as water levels rose and reoccupied these areas when the water level fell. Most of the organisms in the sublittoral zone were in the 4–32 mg weight range with a rather abrupt truncation at 32 mg. The peak in biomass for the profundal zone was at 8–16 mg in May and increased to 16–32 mg from 8 July to 2 September. The abrupt truncation of the biomass size-spectra for the sublittoral and profundal zones of Narrow Lake suggests that sediments alone may not provide sufficient cover from fish predation for larger macroinvertebrates. Alternatively, the absence of organisms >32 mg, particularly in the sublittoral zone, may simply reflect the fact that large burrowing mayflies (e.g. *Hexagenia*) are absent from the lake.

The wide seasonal variation in the biomass size-spectra has a number of causes. Organisms are lost from the community due to emergence of adult insects and post breeding mortality of amphipods (especially *Gammarus lacustris*), snails, psiid clams, and leeches. Emergence of adult insects has less effect on the littoral community because different species emerge at different times, there is continuous growth of long-lived organisms (e.g. odonate nymphs and *Nephelopsis*), there are bivoltine species of chironomids and ephemeropterans present, and some organisms (e.g. *Hyallela azteca*) reproduce almost continuously during the summer months. The complicated food web in the littoral zone and the almost constant input of biomass to the small size-classes due to reproduction greatly reduces the

TABLE 1. Parameters for regression of $\log_2$ (total weight in size-class/weight range in interval) on $\log_2$ (upper limit of size-class) for littoral zone macroinvertebrates collected biweekly in Narrow Lake during 1986. Data cover a range from 1–1024 mg.

Date	Slope	SE of slope	Intercept	SE of intercept	MSE	r^2	n
13 May	−0.89	0.111	10.9	0.691	1.024	0.88	10
27 May	−1.06	0.096	11.9	0.596	0.761	0.94	10
10 June	−0.92	0.126	10.9	0.710	0.955	0.88	9
24 June	−1.00	0.131	11.0	0.810	1.405	0.88	10
08 July	−1.96	0.302	11.3	1.350	2.554	0.89	7
22 July	−0.94	0.139	10.8	0.865	1.604	0.85	10
05 Aug.	−0.86	0.042	10.1	0.260	0.146	0.98	10
19 Aug.	−0.94	0.057	10.8	0.353	0.268	0.97	10
02 Sept.	−0.86	0.074	10.8	0.456	0.446	0.94	10

likelihood that peaks in the biomass size-spectrum will propagate in time through the size-spectrum (Silvert and Platt 1978). There are many fewer taxa in the sublittoral and profundal zone communities, thus the synchronous emergence of chironomids and *Chaoborus* removes a proportionately greater fraction of the total biomass in these zones and, therefore, adds to the variation in the shape of the size-spectra.

The normalized size-spectra allow a simplified view of the seasonal variation in the biomass size-spectra for the littoral zone (Table 1). The amount of variation in the data (r^2) explained by the regressions was high (85–98%) but the residual variation (MSE) varied 17-fold among the regressions. The slopes had a range of −1.96 to −0.86 or −1.06 to −0.86 if the data for 8 July are excluded. The biomass size-spectrum for 8 July was greatly affected by the absence of large organisms in the samples. The biomass size-spectra for 5 August and 19 August were almost flat (Fig. 2) and the normalized size-spectra for these two dates showed the best fit (lowest MSE and highest r^2) to the data. The slopes of the normalized size-spectra appear to be relatively insensitive to variation in the data because the relatively small range of slopes (Table 1) represented wide variation in the shape of the biomass size-spectra. Further, the slopes in Table 1 covered a range as wide as that reported for a variety of pelagic systems which differed greatly in size and productivity (Sprules and Munawar 1986). When comparing biomass size-spectra among ecosystems, it is important to avoid comparing data collected at different times. It is probably best to use data collected concurrently on several sampling dates or, at very least, base the comparisons on seasonal averages.

When averaged across all nine collection dates, the littoral zone biomass size-spectrum had a weak biomass peak at 8–16 mg (16% of the total biomass) and a second weak peak at 256–512 mg (14% of the biomass) (Fig. 3). The sublittoral zone had a single, strong peak at 8–16 mg (30% of the biomass) and the profundal zone had a strong peak at 16–32 mg (34% of the biomass). Residual variation of the normalized size-spectrum for the littoral zone was low (MSE = 0.48) and the slope (−0.95) was not significantly different from −1.0 ($t = 0.66$, $P > 0.05$). The relatively low residual variation around the regression line for the littoral zone was not surprising because the littoral zone supports a diverse food web that can have herbivores, detritivores, and predators within all size-classes. Furthermore, some taxonomic groups (e.g. amphipods and gastropods) are polytrophic. The regression for the average sublittoral zone data had more unexplained variation (MSE = 3.113), but the slope (−1.16) was not significantly different from −1.0 ($t = 0.48$, $P > 0.05$). The greater variation in the sublittoral zone data probably reflects the proportionately greater effect of events such as emergence of chironomids in a community with fewer species. The slope (−0.02) of the regression for the profundal zone data was not significantly different from 0.0 ($t = -0.13$, $P = 0.9$), probably due to the simple community and narrow size-range or organisms. In addition, Narrow Lake is partially meromictic (Trimbee and Prepas 1988) and lacks organisms such as *Ponteporia* and *Mysis* that complete their entire life cycle in the profundal zone.

Unionid clams dominated the total biomass and biomass size-spectra of macroinvertebrates in Narrow Lake. The biomass of clams >10 mm long on the littoral zone, corrected for the 20% of the littoral zone where clams do not occur (Hanson et al. 1988a), was 124 g/m^2 compared with 14.6 g/m^2 for the rest of the macroinvertebrates. Clams clearly dominated the biomass size-spectrum for the littoral zone (Fig. 4). The peak for clams in the 16.3–32.8 g size-class (67.6 g/m^2) dwarfs the peak for the other macroinvertebrates at 8–16 mg (2.3 g/m^2). The biomass peak for unionid clams was truncated. Very few clams >70 mm long (22 g wet weight) were found in Narrow Lake despite the fact that *Anodonta grandis* often attains lengths >90 mm (47 g wet weight) in other waters (Green 1980; McCuaig and Green 1983; J. M. Hanson et al., unpubl. data). This absence of large clams is likely the result of size-selective predation by muskrats (*Ondatra zebithicus*). During 1986/87, muskrat predation on clams >70 mm long exceeded the annual production of this size-class by an amount equivalent to 10% of the biomass and if this predation rate persists, clams >70 mm long could be eliminated from the lake (Hanson et al. 1989).

The inclusion of the data for unionid clams greatly affected the normalized size-spectra for the littoral zone community (Fig. 4). The slope of the regression (−0.65) was significantly different from −1.0 ($t = 4.61$, $P < 0.001$) and the amount of residual variation increased fourfold (MSE = 1.632). It is not clear whether unionid clams should be included in the size-spectra for macroinvertebrates because clams use a different food resource than most other littoral zone macroinvertebrates and are largely immune from predation; they probably only enter the littoral food chain as detritus upon death. Clams feed by filtering suspended materials from the water and, therefore, interact with the pelagic community. Given the low filtering rates of freshwater clams (Lewandowski and Stanczykowska 1975; Paterson 1986), the clam population in Narrow Lake would require 4 yr to filter a volume equivalent to the epilimnion (Hanson et al. 1988b). Thus the impact of clams on the pelagic community is minor because the turnover time for the

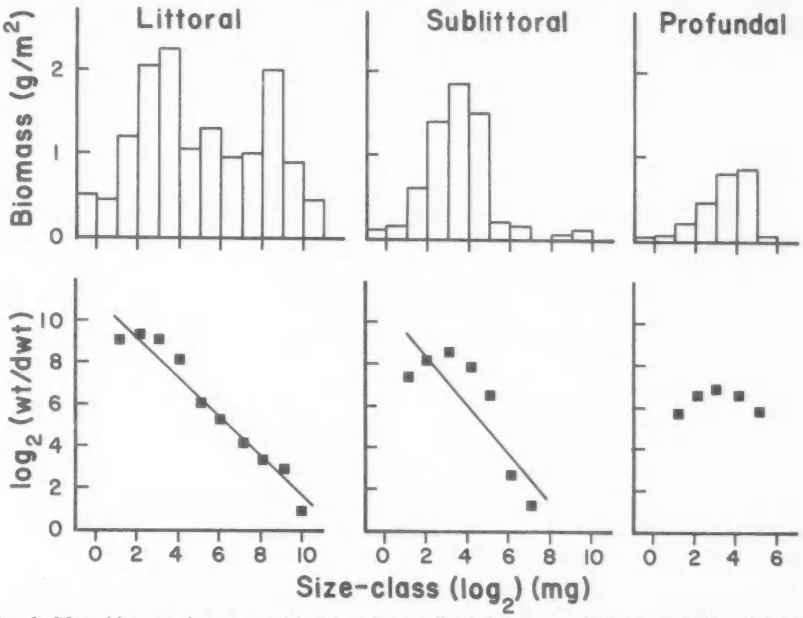

FIG. 3. Mean biomass size-spectra (above) and normalized size-spectra (below; regression of (total weight in size-class)/(weight range in interval) on upper limit of size-interval) for the macroinvertebrate communities (minus unionid clams) of the littoral, sublittoral, and profundal zones of Narrow Lake during 1986. The regression for the littoral zone was: $Y = 11.0–0.95\ X$, $n = 10$, $r^2 = 0.95$, SE of slope = 0.076, SE of intercept = 0.471, $MSE = 0.476$, $P < 0.001$. The regression for the sublittoral zone was: $Y = 10.6 - 1.16\ X$, $n = 7$, $r^2 = 0.71$, SE of slope = 0.333, SE of intercept = 1.491, $MSE = 3.113$, $P = 0.018$. The slope of the regression for the profundal zone not significantly different from 0.0.

plankton is several orders of magnitude faster than the rate at which clams remove them.

There was a peak in the 8–16 mg weight-class (1.5 g/m^2) for the whole-lake biomass size-spectrum (Fig. 5). This peak is not unexpected because there was a peak at or near the 8–16 mg weight-class for all three depth zones (Fig. 3). Since there were few organisms >64 mg in weight in the sublittoral and profundal zones, the biomass peak at 256–512 mg from the littoral zone was greatly reduced (to 0.4 g/m^2) in the overall size-spectrum (Fig. 5). Unionid clams still dominated the overall size-spectrum, although the height of the peak (13.9 g/m^2) was reduced because clams are seldom found at depths <6 m in Narrow Lake (Hanson et al. 1988a,b). The biomass size-spectra for Narrow Lake are similar to the size-spectra reported for marine benthic communities. Marine benthic size-spectra are generally trimodal with peaks that roughly correspond to bacteria, meiofauna, and macrofauna (Schwinghamer 1981, 1985; Gerlach et al. 1985). Schwinghamer (1981, 1985) reported that the macrofauna biomass peaks for a number of marine benthic communities varied from the 1–2 mg to the 1.2–9.7 g classes; the position of the peaks apparently depends upon the existence of bivalves on the site. Unlike the marine communities, available data for freshwater benthic communities do not show a peak for meiofauna (Strayer 1986; Cattaneo 1987) but the data are too few to conclude meiofauna are less abundant in freshwater ecosystems.

In Narrow Lake, the slope of the normalized size-spectrum (minus unionid clams) (Fig. 5) for the whole-lake (−1.12) did not differ significantly from −1.0 ($t = 1.02$, $P > 0.05$). However, the amount of unexplained variation (MSE = 1.156) was almost three times that of the regression for the littoral zone alone. This reflects the variation in the sublittoral and profundal zone data. Since the overall size-spectrum is based on area weighted data for the three depth zones, the effect of a larger or smaller littoral zone would be to make the overall size-spectrum more or less similar, respectively, to the size-spectrum for the littoral zone and the size of the residual variation will also reflect the weight of the littoral zone data. The inclusion of unionid clams again greatly affected the normalized size-spectra. With clams, the slope of the overall regression (−0.78) was significantly different from −1.0 ($t = 2.37$, $P < 0.01$) and the amount of residual variation more than doubled (MSE = 2.45).

We made a preliminary assessment on whether there is roughly equal biomass in six of the major functional groups of organisms in Narrow Lake (Table 2). For both the littoral zone and whole-lake comparisons, the greatest amount of biomass was in the macrophytes. When macrophyte data are omitted, there was more biomass in the clams than in the remaining groups combined. Even after the clams are omitted, biomass of organisms in the littoral zone still was not evenly distributed among the remaining four functional groups: the biomass of macroinvertebrates exceeded that of the other three groups combined, including fish. Although fish depend directly upon macroinvertebrates for food, macroinvertebrate biomass generally exceeds fish biomass in the littoral zone (Post and Cucin 1984; Boisclair and Leggett 1985; Hanson and Leggett 1986), probably due to the fact that only a very small fraction of the macroinvertebrates present are available to fish predation (Boisclair and Leggett 1985). This differs from the pelagic zone

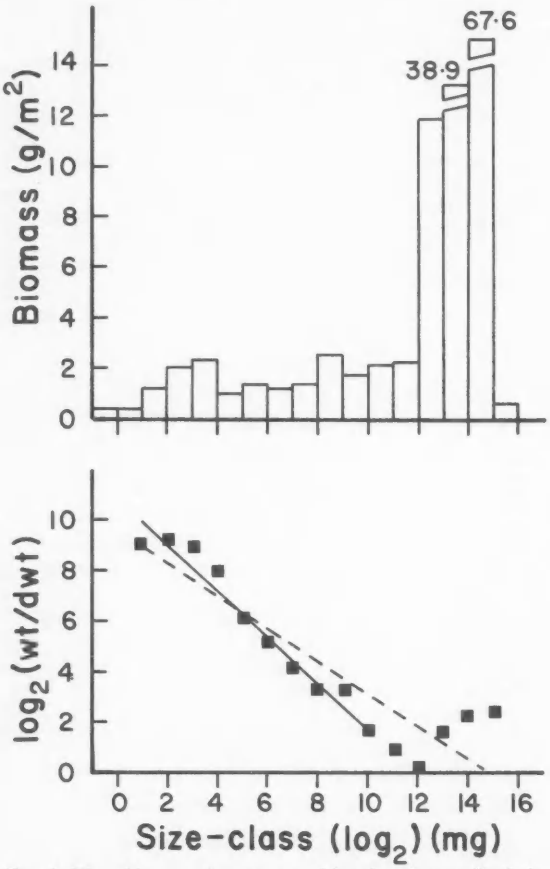

FIG. 4. Mean biomass size-spectrum (above) and normalized size-spectrum (below; regression of (total weight in size-class)/(weight range in interval) on upper limit of size-class) for the macroinvertebrate community (including unionid clams) of the littoral zone of Narrow Lake during 1986. The solid line is the normalized size-spectrum excluding unionid clams, the dashed line includes clams. The regression for the littoral zone with clams was: $Y = 9.61 - 0.65\,X$, $n = 15$, $r^2 = 0.85$, SE of slope = 0.076; SE of intercept = 0.694, $MSE = 1.632$, $P < 0.001$.

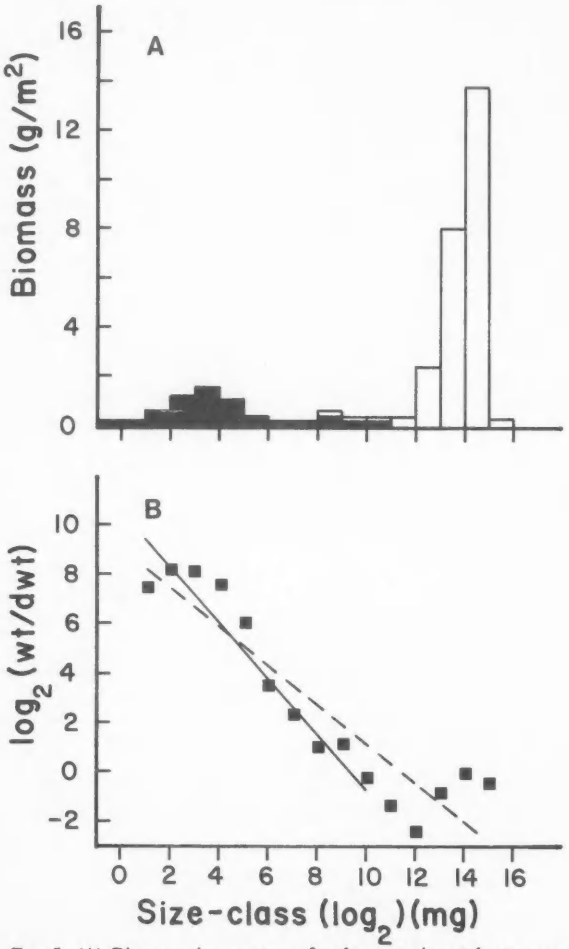

FIG. 5. (A) Biomass size-spectrum for the macroinvertebrate community of Narrow Lake based on area-weighted means for the littoral, sublittoral, and profundal zones. Solid bars represent macroinvertebrates minus unionid clams, open bars represent unionid clams >age − 1. (B) Normalized size-spectra (regression of (total weight in size-class)/(weight range in interval) on upper limit of size-class) for the whole-lake macroinvertebrate community of Narrow Lake. The solid line represents the data minus unionid clams. The regression was: $Y = 10.52 - 1.12\,X$, $n = 10$, $r^2 = 0.92$, SE of slope = 0.118, SE of intercept = 0.734, $MSE = 1.156$, $P < 0.001$. The dashed line represents the data for the macroinvertebrate community plus unionid clams. The regression was: $Y = 8.93 - 0.78\,X$, $n = 15$, $r^2 = 0.84$, SE of slope = 0.093, SE of intercept = 0.850, $MSE = 2.447$, $P < 0.001$.

where most of the crustacean zooplankton present are vulnerable to fish predators and a linear relationship between zooplankton and pelagic fish biomass is, therefore, expected. On a whole-lake basis, the biomass of zooplankton and macroinvertebrates was very similar. When making comparisons among lakes, it is essential to consider that the size of the various depth zones will greatly affect the relative biomass in the various functional groups. For example, doubling the littoral zone area in Narrow Lake would increase the whole-lake biomass of macroinvertebrates and clams to 8.5 g/m^2 and 50.8 g/m^2, respectively, but would decrease the biomass of phytoplankton and zooplankton in proportion to the decrease in lake volume. Conversely, a smaller littoral zone will result in a proportionately greater biomass of phytoplankton and zooplankton and a proportionately smaller biomass of macroinvertebrates and unionid clams. Thus lakes which have similar nutrient levels or chlorophyll *a* concentrations could differ greatly in their overall biomass size-spectra due to relative differences in littoral zone area. We suggest the offshore and littoral communities are best analysed separately, especially as the two zones differ substantially in energy inputs and losses (see below).

General Discussion

The biomass size-spectra for Narrow Lake have a number of features which should be characteristic of most temperate and north temperate lakes and one feature, the absence of crayfish, which is characteristic of Alberta lakes.

TABLE 2. Biomass (grams per square metre, fresh weight) of phytoplankton, macrophytes, zooplankton, macroinvertebrates, unionid clams, and fish in Narrow Lake. Phytoplankton estimates are from Trimbee and Prepas (1988) and assume chlorophyll $a = 0.01$ wet biomass (McCauley and Kalff 1981). Macrophyte samples are based on five sites sampled on each of six transects during July and August 1985 ($n = 30$, E.E. Prepas, unpubl. data). Zooplankton represent seston <64 μm (Prepas and Vickery 1984; E.E. Prepas, unpubl. data). Littoral fish biomass was based on 16 seine samples taken by methods described in Hanson and Leggett (1985) (W.C. Mackay and J.M. Hanson, unpubl. data).

Functional group	Littoral zone biomass	Whole-lake biomass
Phytoplankton	0.8	2.2
Macrophytes	256.7	52.6
Zooplankton	1.3	6.6
Macroinvertebrates	14.6	6.3
Unionid clams	123.9	25.6
Fish	2.6	1.5[a]

[a]Assumes littoral biomass = sublittoral biomass; no fish in profundal zone.

Seasonal variation in the size-structure of the macroinvertebrate community was wide in Narrow Lake and is likely so in other lakes. The amount of variation will depend on the life history characteristics of the species within a given lake especially in regards to the number of generations/year and the degree to which insect emergences are synchronous. In particular, our data for 8 July 1986 illustrates the potential bias possible in making comparisons among lakes if collections taken on a single date are assumed to be representative of the macroinvertebrate community. However, it would be extremely tedious to compare size-spectra among lakes if data must be collected biweekly. To address this problem, we compared normalized size-spectra based on averages of data collected at 4- and 6-wk intervals to the regression based on biweekly samples (Table 3). All of the regressions were very similar, and we conclude that data based on 4- or 6-wk sampling intervals adequately represent the seasonal average size-distribution for the littoral zone.

The large differences between size-spectra for the littoral zone macroinvertebrate community and the size-spectra for the other two zones reflect fundamental differences in habitats and energy cycling. The littoral zone is a much more complex habitat than the sublittoral and profundal zones and provides much more structural cover from fish predation for all sizes of macroinvertebrates. Boisclair and Leggett (1985) estimated, on a daily basis, that <1% of the macroinvertebrates present in the littoral zone could be eaten by fish. Furthermore, Hanson and Leggett (1986) showed experimentally that littoral zone fish lost weight if stocked at higher than natural densities and that neither total abundance nor the abundance of the major prey species was negatively affected by the higher fish densities. In addition, there is more food for macroinvertebrates in the littoral zone. Macroinvertebrates obtain food from allochthonous material, macrophytes and epiphytes, and phytoplankton (Rau 1980; Timms 1980; Danell and Anderson 1982; Rasmussen 1982; Cattaneo 1983; Kairesalo and Koskimies 1987). The littoral macroinvertebrate community can draw on all three food sources directly whereas the sublittoral and profundal communites must depend on sedimentation of phytoplankton and transport of detritus from the littoral zone. Finally, all three depth zones lose macroinvertebrates through emergence of adult insects, but the littoral zone also loses a significant, but unknown, fraction of macroinvertebrate production to waterfowl predation (Eadie and Keast 1982; Brown and Fredrickson 1986; Gauthier 1987). This linkage with terrestrial inputs and losses clearly separates the littoral community from the pelagic community, and we think the two should be analysed separately.

Unionid clams dominated both the total biomass and the size-structure of the macroinvertebrate community in Narrow Lake. Unionid clams are seldom collected in quantitative surveys of macroinvertebrates. The few data that exist for other lakes indicate that unionid clams make up a large fraction of the biomass of benthic communities (Okland 1963; Kajak and Dusoges 1975; Fisher and Tevesz 1976) and we expect the biomass size-spectra of many lakes will be dominated by clams. Our data support with the argument of Schwinghamer (1981) that benthic biomass should accumulate in slow-growing filter feeders that are largely immune from predators. This argument may not apply to lakes that contain crayfish.

Crayfish are absent from Narrow Lake and most lakes in Alberta. *Orconectes virilis* is the crayfish normally found in northern lakes (Crocker and Barr 1968) and it attains a maximum size of 20–25 g (Momot 1967; Lodge and Lorman 1987). Even at the densities typically found in Precambrian shield lakes (0.6 to 2 adults/m^2, France 1985), crayfish will greatly increase the biomass of large organisms in the benthic size-spectrum. Like clams, adult crayfish often have a few fish predators (Stein 1977; Gowing and Momot 1979; Hepworth and Duffield 1987) but, unlike clams, crayfish are an important part of the littoral community as a detritivore, herbivore, and even a predator on other macroinvertebrates (Momot et al. 1978; Capelli 1980; Lodge and Lorman 1987). Although crayfish are seldom collected quantitatively in benthic surveys, variation in their abundance can be expected to have a major effect on the structure of the macroinvertebrate community.

TABLE 3. Parameters of normalized size-spectra for the littoral macroinvertebrate community (minus unionid clams) based on data collected at 2-(regression 1), 4-(regressions 2 and 3), and 6-(regressions 4, 5, and 6) wk intervals. Regressions 1, 3, and 5 include the data for 8 July 1986. All regressions were significant at $P < 0.001$.

No. of collections	Slope	SE of slope	Intercept	SE of intercept	MSE	r^2	n
9	−0.95	0.076	11.0	0.471	0.476	0.95	10
4	−0.99	0.090	11.2	0.557	0.664	0.94	10
5	−0.95	0.084	10.3	0.524	0.589	0.94	10
3	−0.92	0.077	10.7	0.477	0.487	0.95	10
3	−1.04	0.095	10.4	0.589	0.743	0.94	10
3	−0.94	0.085	11.0	0.530	0.602	0.94	10

Our data indicate that biomass size-spectra and normalized size-spectra are useful comparative tools to evaluate the structure of macroinvertebrate communities. The results suggest that the various depth zones are best analysed separately. It is unknown whether the size-structure of macroinvertebrate communities will vary across lakes in a systematic fashion similar to that described by Sprules and Munawar (1986) for pelagic communities because comparable data for lentic invertebrate communities are not available.

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Environmental Complexity and the Drifting Behaviour of a Running Water Amphipod

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Williams, D. D., and K. A. Moore. 1989. Environmental complexity and the drifting behaviour of a running water amphipod. Can. J. Fish. Aquat. Sci. 46: 1520–1530.

Overall level and type of activity of *Gammarus pseudolimnaeus* changed with current speed and pattern in laboratory stream tanks. With increasing current speed (15 to 28 cm/s) active and passive downstream transport increased, whereas numbers of animals moving upstream decreased. Upstream movement increased in smooth and rough flow above 28 cm/s. Mean swimming speeds of individuals differed between day and night at most current settings. Total distances drifted by single animals were greater in 43-L ("macroenvironments") than in 3.5-L stream tanks ("microenvironments"), and were greater in both environments at night. On average, individuals had 6.8 drift episodes during 12 h darkness in microenvironments (nightly downstream displacement 3.04 m), compared with 37.9 episodes in macroenvironments (displacement 22.4 m). Level of activity was positively related to amphipod benthic density during both day and night in microenvironments; however, in macroenvironments, at night, the relationship was negative. Cessation of drift in the presence of fish predators and marked nocturnal activity peaks in macroenvironments were absent in microenvironments. The different responses within the two environments may reflect differences in perception of local environmental scale by the amphipods. This process may occur during the periodic contacts that animals make with the substrate during drift; individuals may retain some familiarity with features of their immediate surroundings.

Des études menées en laboratoire dans des bassins ont montré que le niveau global d'activité et le type d'activité de *Gammarus pseudolimnaeus*, varient en fonction de la vitesse et du type de courant. Quand la vitesse du courant augmente (15 à 28 cm/s), le déplacement actif et passif des gammares augmente tandis que le nombre de gammares qui se déplacent à contre-courant diminue. Le déplacement des gammares à contre-courant augmente dans des conditions d'écoulement laminaire et turbulent à des vitesses de courant supérieures à 28 cm/s. Dans la plupart des conditions de courant, les vitesses moyennes de nage des individus n'étaient pas les mêmes le jour et la nuit. Les distances totales parcourues par les individus étaient supérieures dans le bassin de 43-L («macromilieu») à celles parcourues dans les bassins de 3,5-L («micromilieu»); elles étaient aussi supérieures, dans les deux milieux, durant la nuit. En moyenne, le nombre de périodes de dérive des gammares durant les 12 h de nuit était de 6,8 dans le micromilieu (déplacement nocturne vers l'aval de 3,04 m), comparé à 37,9 périodes dans le micromilieu (déplacement de 22,4 m). Dans les micromilieux, le niveau d'activité augmentait avec la densité des amphipodes au fond des bassins aussi bien le jour que la nuit; cependant, dans les macromilieux, cette relation était inversée durant la nuit. Dans les micromilieux, il n'y avait pas arrêt des déplacements quand des poissons prédateurs étaient introduits dans le bassin et nous n'avons pas observé de maximums d'activité prononcés durant la nuit comme il a été observé dans les macromilieux. Les différences de comportement qui ont été observées dans les deux milieux pourraient être attribuables à des différences relatives à la perception qu'ont les amphipodes de leur environnement. Ce processus pourrait avoir lieu durant les contacts périodiques que les gammares ont avec le substrat au cours de leur déplacement : les caractéristiques de l'environnement immédiat des gammares pourraient déterminer leur niveau d'activité.

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Despite several decades of research examining stream drift, both in the field and laboratory (Waters 1972), much remains that we do not understand about the role of physical and biological factors in controlling the drift process (Statzner et al. 1984). Several abiotic factors are known to correlate with drift density, these are discharge, water temperature, and photoperiod, but field measurements or experiments involving these factors often produce contradictory results (e.g. Andersson et al. 1986; Culp 1986; Perry and Perry 1986; Statzner et al. 1987). These inconsistencies may be partially due to qualitative and quantitative differences in the composition of benthic communities between streams (D. D. Williams, unpubl. data).

There is also a behavioural component to drift, as many species apparently show an active determination to enter and leave the water column with a definite periodicity (Müller 1974). This component may differ in intensity among species. "Behavioural drift" may be supplemented or, over-shadowed by animals drifting as the result of various abiotic factors such as the above mentioned. This had led to the proposal of additional categories of drift. For example, "catastrophic drift" results from physical disturbance of the benthos while "constant drift" occurs more or less continually, but at low level, and may represent animals that accidentally lose their grasp on the stream bed (Minckley 1964; Waters 1965; Williams and Levens 1988). However, another component of "constant drift" in some species may result from voluntary, aperiodic release from the substrate. There may be a behavioural component to "catastrophic drift" as well. Terms have become ambiguous as authors have wrestled with trying to decipher whether or not entry into the

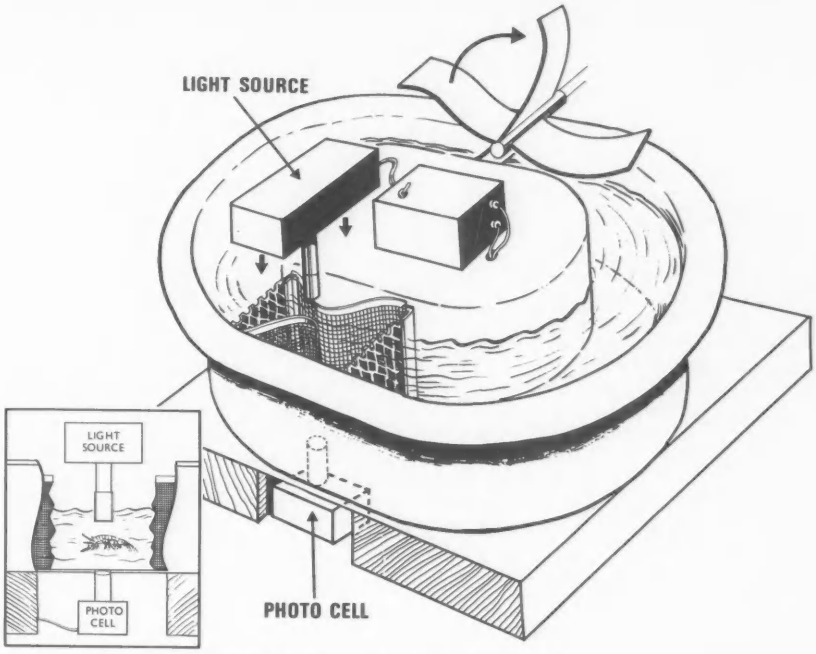


FIG. 1. Diagram of a large activity tank.

drift is an intentional act by an organism. It may be that a single drift episode is comprised of more than one component phase, each affected by different factors, perhaps operating independently. One component might be "entry into the drift", a second, "transport in the water column", and a third, "termination of drift". Each component may be controlled by different behavioural and/or environmental factors. For example, "entry" could be initiated by erosion, whereas "transport" may be more associated with hydrodynamics. Reestablishment on the stream bed during "termination" could be the result of the animal swimming towards the bed (behavioural) or being passively carried towards the bed by gravity or current (environmental). Our future understanding of the causes of drift requires an integrated, experimental approach recognizing that many factors, acting both simultaneously and independently, may be responsible (Wiley and Kohler 1984).

Laboratory experiments in which single species are subjected to the systematic manipulation of environmental variables may contribute to the unravelling of the complexity of factors governing stream drift (Corkum et al. 1977; Williams and Moore 1982). They also may reveal the relative importance of the different types of drift and compensatory upstream migration (Bishop and Hynes 1969).

The purpose of this study was to examine the activity response of a lotic invertebrate (*Gammarus pseudolimnaeus* Bousfield) to laboratory manipulation of local environment and to determine whether drift response could be used to assess the animal's ability to perceive scale in its surroundings. This was done by seeking answers to the following specific questions: (1) do activity level and type change at different current speeds and flow patterns? (2) are there differences in distances moved in the water column ("transport") according to size of environment, and do these vary with light conditions? (3) do activity patterns of single animals change at different population densities and according to light regime in small versus large environments? (4) does the response to predators vary with size of environment?

Methods

The experiments were conducted in oval, recirculating, laboratory stream tanks held in environmental chambers at 12°C. The tanks were of two sizes, 43-L (length of channel on midline = 250 cm; channel width = 14.5 cm), described by Williams and Moore (1982), and smaller, 3.5-L (length of channel = 55 cm; channel width = 7.3 cm). Each tank (Fig. 1) had a small plexiglass window (2.0 × 12.0 cm) across the bottom of the channel on the side opposite the paddle wheel. Two curved 2-mm mesh brass screens formed a narrow passage 1.8 cm wide in mid channel over the window. Two removable end screens of 1.5-cm mesh ensured that only *Gammarus* could pass through this section of the tank.

Movement through this passage was monitored automatically by ultraviolet beam interruption (Wallace et al. 1975). A metal box containing the light source and holding a copper tube (1.8 cm diameter and 9.8 cm long) channeled the light into a cylindrical beam shining vertically down into the water. The copper tube was enclosed in a glass vial, to prevent direct contact with the water, and was aligned over the centre of the plexiglass window. Beneath the channel, directly under the light, a second copper tube contained an ultraviolet photocell lined up with the beam. The tube provided shading from extraneous light. Passage of animals through the beam was recorded as a line on the paper of a chart recorder operated at a speed of 3 mm/min. The electronic circuitry was specifically designed so that the amount of time spent in the beam was proportional to the length of line

TABLE 1. Summary of treatment conditions.

Experiment	Treatment conditions	Type of observation	Periodicity	Tank size	*N*
Effect of current velocity on:					
(1) Activity level	— Five current velocities (15–40 cm/s)	Monitoring system	Night	Large	Three trials
(2) Type of activity	— Six current velocities (0–40 cm/s)	Monitoring system	Day and night	Large	500–550 observations
Determination of distance drifted	— Total distance drifted per drift episode (dead and live animals)	Direct observation	Day	Large and small	100–250 observations
	— Distance drifted before first contact with stream walls (dead and live animals)	Direct observation	Day	Large and small	100–250 observations
	— Number of times animal touched before settling (dead and live animals)	Direct observation	Day	Large and small	100 observations
	— Total distance drifted per amphipod	Monitoring system	Day and night	Large and small	40–300 observations
	— Number of drift episodes per individual per night	Monitoring system	Day and night	Large	30–300 observations
Effects of density on activity level	— Seven density levels (0.002–0.105 animals/cm^2)	Monitoring system	Day and night	Large	10 trials
Effect of predators on activity level	— Fish present	Monitoring system	Night	Large and small	15 trials
	— Fish absent	Monitoring system	Night	Large and small	15 trials

produced on the chart paper. Amphipods moving against the current caused large deflections of the recorder pen (e.g. range 9.0 to 20.5 cm at 15 cm/s), while those swimming with the current caused much smaller deflections (under 2.5 cm at 15 cm/s). Wallace et al. (1975) showed that *G. pseudolimnaeus* were unable to detect ultraviolet light and behaviour was not affected by the beam.

The tanks were illuminated by banks of fluorescent and incandescent lights which provided an illumination of 13.5 $\mu E \cdot s^{-1} \cdot m^{-2}$ under 6 cm of water during the daylight phase of a 12:12 L:D cycle. There was a substrate of medium-sized gravel in the tanks (mean diameter = 11.0 mm) and a water depth of 13 cm. The surface area of the bottom of each large tank was 2068 cm^2 compared with 380 cm^2 for each of the small tanks.

Amphipods were collected from Balsam Creek, Durham County, Ontario (43°59′N, 79°04′W). Densities of amphipods (adults of both sexes) per unit area and food in the tanks were kept the same at 20 animals/large tank and four animals/small tank. The diet consisted of pelleted rabbit food, which was readily consumed by *G. pseudolimnaeus* and allowed growth.

The various experimental manipulations are summarized in Table 1.

Effect of Current Velocity on Activity

Activity responses to manipulation of current speed and flow pattern were measured only in the large tanks. Manipulation was achieved by increasing the rotation of the paddle wheel to give currents of 15, 28, and 40 cm/s. Water flow at these speeds was relatively laminar as determined by the mixing patterns of dye in the water column. At maximum rotation a very rough pattern flow was produced. Measured current speed at this setting was also approximately 40 cm/s. Nocturnal activity was recorded at each current speed, in three replicate trials of 10 consecutive hours each. Data from the 2 h around dusk and dawn were not used because of the high variance in counts in these transitional periods (see Fig. 9). Fresh animals were used in each trial.

Since terminology within the drift literature is in a somewhat confused state, we partitioned the activity that we observed into four types: "active downstream transport", "passive downstream transport", "upstream movement", and "exposed", according to the length of time that each animal took to travel through the 1.8-cm diameter light beam of the activity tank, which was recorded by length of lines of trace on the chart. At each current speed, the range of times (in relative units) to traverse the light beam of passively transported animals was defined by measuring the times taken by freshly-killed animals. For example, the range of data (normally distributed) for 15 cm/s was (normally distributed) two to eight time units (Fig. 3). Our definition of "passive downstream transport" differs somewhat from that of "passive drift" (e.g. Wiley and Kohler (1984) ". . .passive entry is presumably the result of accidental or unintentional release, and subsequent errosion. . ."). Our definition refers solely to how the animals move in the water column with no assumption of motivation behind release from the substrate. Animals undergoing "active downstream transport" were defined as those swimming with the current and passing through the light beam at speeds faster than passively transported animals; in this example, zero to two time units at 15 cm/s. Animals engaged in "upstream movement" against the current took longer than passively transported animals to cross the light beam (range nine to 20.5 time units). A small percentage of animals sat or crawled on the screens directly under the photocell for periods of >21 time units (determined by direct observation). These have been termed "exposed".

Determination of Distances Drifted

Distances drifted and times spent in the water column were obtained by direct observation of the point of entry into the drift by individual amphipods, the distance to first contact with the tank walls, the number of times the walls were contacted before

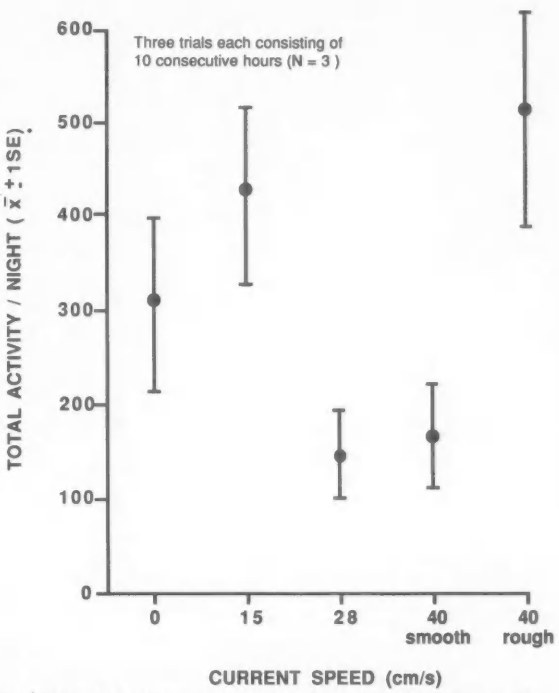


FIG. 2. Total activity level (all categories combined) of 20 adult *Gammarus pseudolimnaeus* of mixed sexes under different current regimes (large stream tanks).

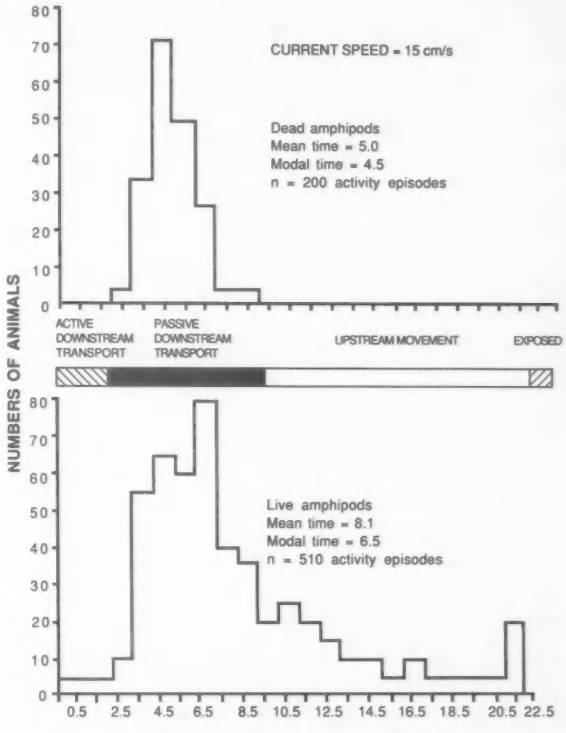


FIG. 3. Frequency distribution of the various times taken for single amphipods to pass through the light beam at a current of 15 cm/s (large stream tanks) (Time is in relative units as passage times through the light beam were recorded as lines of various length on a chart recorder, see methods; n = number of activity episodes of individual amphipods monitored which was targeted at between 200 and 550).

the animal finally settled, and distance of each total drift episode. These variables were measured in both the large and small tanks under standard tank conditions. In order to distinguish behavioural from physical responses, these procedures were repeated using freshly-killed amphipods. Neither live nor dead amphipods seemed to be affected when going through the passage between the two screens.

Effect of Density on Activity Level

Estimates of the activities of single amphipods at different population densities (at constant current) were calculated from the total number of activities recorded per 10-h period divided by the appropriate number of animals in the tank. This necessitated assuming that the activity level of each animal within a single trial was similar. For these trials, the range of densities in the small tanks was from 1–40 per tank, while in the large tanks it was 4–220. Comparisons between tank size and day–night activity were made using linear regression based on replicated values of the dependent variable ($n = 10$).

Effect of Predators on Activity Level

A number of small, similar-sized (approximately 7 cm long), caged dace (*Rhinichthys* sp.) were introduced to amphipod environments of different size (1/small tank; 5/large tank) 3 h after the lights went out, a time when amphipod activity was high (Williams and Moore 1982).

Statistical tests were performed on ln-transformed data in order to conform with test prerequisites of normality and homoscedasticity.

Results

Activity Level and Type of Drift Transport at Different Currents

Increasing current speed from 0–40 cm/s, showed a response in activity similar to that obtained by Williams and Moore (1982) over part of this range (Fig. 2). Activity was higher at zero current and at 15 cm/s than at higher speeds, with 28 cm/s appearing to be optimal, in the sense that this was the speed at which the animals moved least. There was a markedly significant increase ($p<0.0001$, t-test) in activity in flow that was turbulent compared with that which was smooth, even though the mean current speeds were the same. Response in terms of the type of activity also changed with current.

Details of the activity types at different current speeds are shown in Figs. 3, 4, 5, and 6. A summary of the changes of the relative proportion of each of the activity types is shown in Fig. 7. There was an increase in the proportions of animals being transported both actively and passively downstream with an increase in current from 15 to 28 cm/s, but a decrease in the proportion of animals moving upstream. Above 28 cm/s, in both smooth and rough flow conditions, upstream movement increased but the percentage exposing themselves to the current declined. The proportions of amphipods drifting also decreased at high flow.

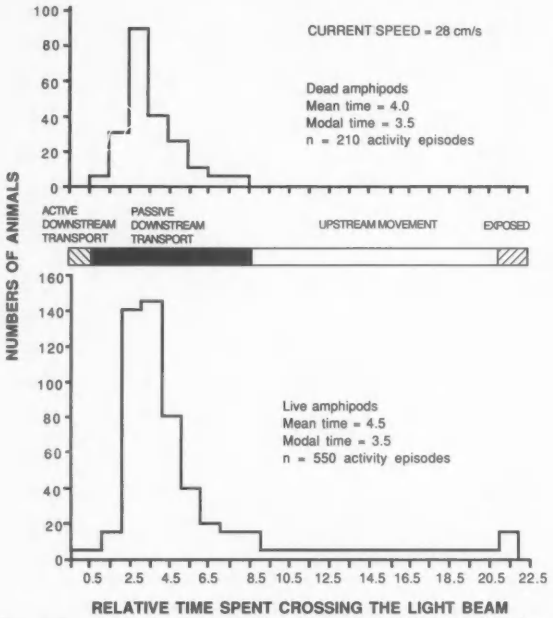


FIG. 4. Frequency distribution of the various times (relative units) taken for single amphipods to pass through the light beam at a current of 28 cm/s (large stream tanks).

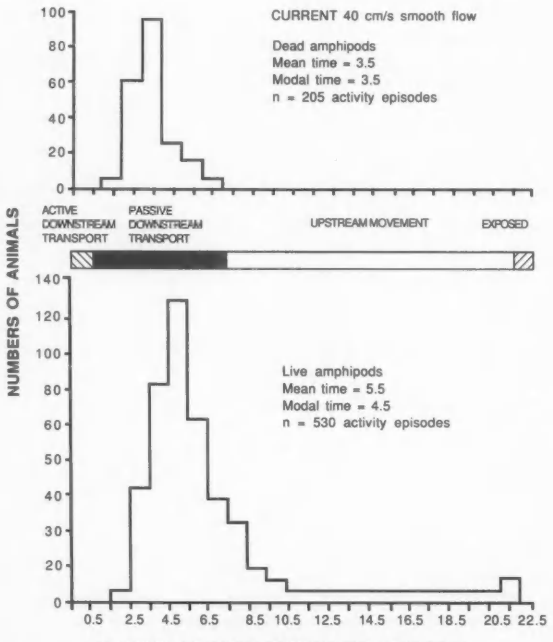


FIG. 5. Frequency distribution of the various times (relative units) taken for single amphipods to pass through the light beam at a current of 40 cm/s (smooth flow; large stream tanks).

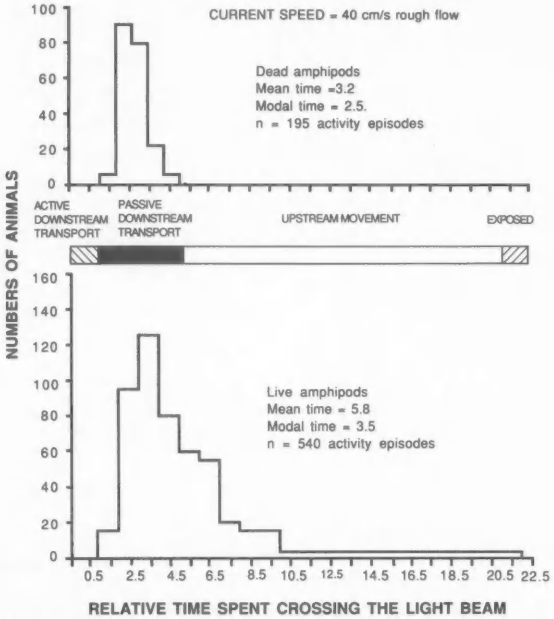


FIG. 6. Frequency distribution of the various times (relative units) taken for single amphipods to pass through the light beam at a current of 40 cm/s (rough flow; large stream tanks).

All the above observations were made at night when *G. pseudolimnaeus* is most active. At zero current however the animals showed increased daytime activity (Fig. 8). The modal times taken to pass through the light beam were the same, in both darkness and light (>21 units), indicating that the amphipods spent a considerable amount of time sitting exposed on tank screens. However, the proportion of exposed animals was much greater during the day (3.2 times). During the day, the mean time taken to pass through the beam was 17.0 ± 0.48 ($\pm$ 1SE) units compared with 13.6 ± 0.23 at night. These two values were significantly different ($p<0.001$, t-test) indicating that the animals swam faster at night (Table 2). Individual amphipods swam faster in the daytime ($p<0.001$, t-test; Table 2) at current speeds of 15 and 28 cm/s. At 40 cm/s, under relatively smooth flow, the animals appeared to swim faster at night, although the daytime data available are limited. At 40 cm/s, under rough flow, there was no statistically significant difference between day and night swimming speed.

Variation in Drift According to Size of Environment

Total distance drifted by a single amphipod in one entire drift episode (i.e. the distance covered from the time of entry into the drift to the time of termination) was significantly greater in the large stream tanks than in the small tanks (approximately 31.0% farther; $p<0.0001$, t-test; Table 3). Similarly, the mean distance drifted before the animals first contacted the tank wall or bottom substrate (but carried on drifting) was greater (83.2% greater; $p<0.0001$, t-test) in the large tanks. The mean number of times an amphipod touched the tank walls or substrate/centimetre drifted was the same in both small and large tanks (Table 3). However, dead animals touched the sides significantly less often ($p<0.005$, t-test) in the large tanks.

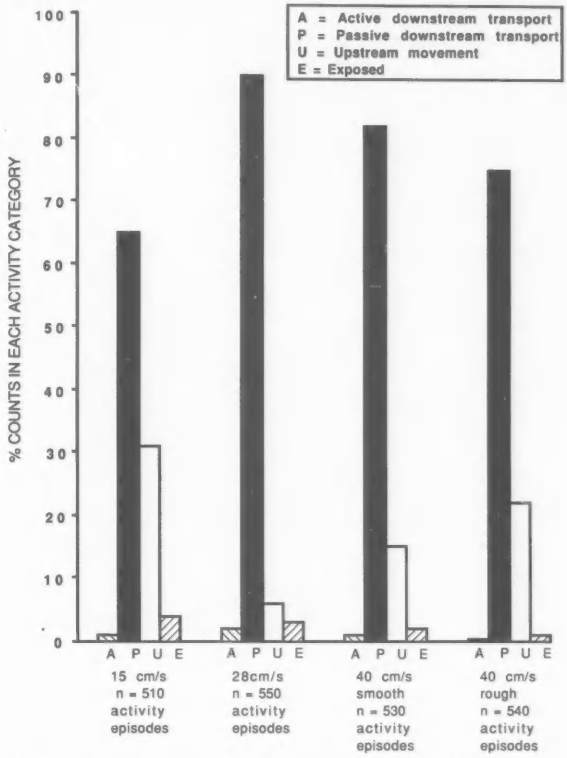

A = Active downstream transport
P = Passive downstream transport
U = Upstream movement
E = Exposed
% COUNTS IN EACH ACTIVITY CATEGORY
A P U E
15 cm/s n = 510 activity episodes
28cm/s n = 550 activity episodes
40 cm/s smooth n = 530 activity episodes
40 cm/s rough n = 540 activity episodes

FIG. 7. Comparative summary of the changes in the relative proportions of each of the four activity types according to current regime (large stream tanks).

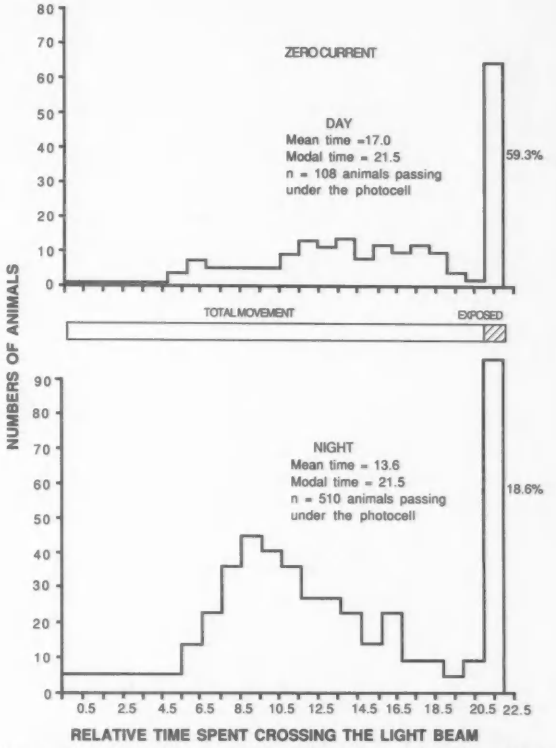


FIG. 8. Comparison between day and nighttime activity of amphipods at zero current (large stream tanks) (n = number of activity episodes of individual animals automatically timed going through the light beam).

Total distance drifted by an animal during 12 h of light or darkness was estimated by dividing the total number of activity events recorded over the time period by the number of amphipods in the tank and multiplying the quotient by the linear distance around the tank. In daylight, the mean distance drifted by individual amphipods in the large tanks was 7.8 times that in the small tanks; at night it was 7.5 times greater in the large tanks. In the small tanks, individuals drifted farther (31.4%; $p<0.001$, t-test) at night than in the day and this was true also for the animals in the large tanks (27.5% farther at night; $p<0.005$, t-test).

Another major difference between the activity patterns of the animals in the large and small tanks was the loss of the marked nocturnal peak in activity normally obtained in both the large tanks (despite equivalent animal densities) and in nature (Fig. 9).

Activity of Single Amphipods at Different Densities

Activity levels at densities from 0.002 to 0.105 animals/cm^2 of bottom substrate in the large and small tanks are shown in Table 4. Regression lines for activity versus density in the small tanks show a significant ($p<0.0001$) positive relationship during both day and night, with a difference in line elevation but not slope (Fig. 10). Density explained some 34.3% of the variance in activity at night and 20.5% during the day.

In the large tanks, the relationship between activity and density was positive during the day but negative at night (Fig. 10).

TABLE 2. Time taken for amphipods to traverse the light beam during the day and night under standard tank conditions but different current speeds in the large stream tanks.

Current (cm/s)	Time taken to traverse beam[a] Day ($\bar{x}$ ± 1SE; n)	Night ($\bar{x}$ ± 1SE; n)	Probability (from t-test)
0	16.4±0.48 (108)	13.6±0.23 (510)	<0.001
15	4.1±0.15 (200)	8.1±0.20 (510)	<0.001
28	3.0±0.14 (200)	4.5±0.15 (550)	<0.001
40 smooth	6.6±1.19 (20)	5.5±0.14 (530)	<0.001
40 rough	5.7±0.54 (110)	5.8±0.13 (540)	0.5

[a]Time is in relative units as passage times through the light beam were recorded as lines of varying length on a chart (see methods).

Both regressions were significant at $p<0.005$ although, as they only explained a small amount of the variance (14.7 and 13.2%, respectively), the relationships are more probably curvilinear than linear. Linear regression, however, makes comparison of lines easier and indicates differences in both the slopes and elevations of the lines for day versus nighttime activity.

There are significant differences in the slopes ($p<0.001$, F-test) and elevations of lines (t-test, $p<0.001$) for the large and small tanks for both day and night, with activity levels in the small tanks frequently being higher than those in the large tanks despite identical densities (Table 4).

TABLE 3. Measured differences in drift parameters between large (43-L) and small (3.5-L) stream tanks under standard tank conditions of 11.0-mm diameter substrate, 13-cm depth of water, current of 15 cm/s and density (20 animals/large tank, 4 animals/small tank).

	Small stream tank ($\bar{x}$ ± 1SE) (n = number of drift episodes)	Large stream tank ($\bar{x}$ ± 1SE) (n = number of drift episodes)	Probability (from t-test)
Total distance drifted[a] by single amphipod in one drift episode (cm) [dead amphipods]	45.1 ± 2.4 (155) [224.0 ± 29.4 (100)]	5.9 ± 2.2 (139) [482.5 ± 61.9 (100)]	<0.0001 <0.0001
Distance drifted before[a] first contact with tank wall (cm) [dead amphipods]	25.6 ± 3.7 (252) [19.4 ± 1.5 (100)]	46.9 ± 1.9 (231) [32.9 ± 2.2 (100)]	<0.0001 <0.0001
Number of times amphipod[a] touched tank wall or substrate/cm drifted [dead amphipods]	0.06 ± 0.006 (100) [0.05 ± 0.006 (100)]	0.06 ± 0.01 (100)] [0.03 ± 0.004 (100)]	>0.05 <0.005
Total distance drifted by a single amphipod during 12 hr of daylight (m)[b]	2.27 ± 0.13 (398)[c]	17.77 ± 0.78 (48)[c]	<0.001
Total distance drifted by a single amphipod during 12 hr of darkness (m)[b]	3.04 ± 0.18 (372)[c]	22.37 ± 1.24 (36)[c]	<0.001
Approximate number of drift episodes/individual/night	6.8	37.9	

[a]Based on direct observations during daylight.

[b]Estimated by dividing the total number of activity events recorded by the photocell over the time period by the number of amphipods in the tank and multiplying the product by the linear distance around the tank.

[c]Differences between these pairs significant at $p<0.05$.

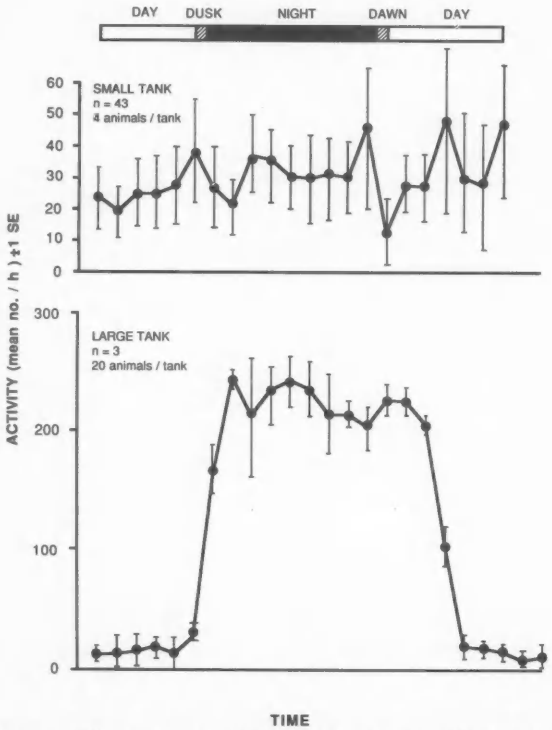


FIG. 9. Difference between diel activity patterns of amphipods in the small and large stream tanks (n = number of trials with fresh animals).

TABLE 4. Summary of the nocturnal activity levels of single amphipods at different densities in large (43-L) and small (3.5-L) stream tanks under standard tank conditions of substrate, depth and current.

		Activity/10 h (± 1SE; n = 10)	
Density/cm^2	Period	Small stream tank (density/tank)	Large stream tank (density/tank)
0.002	Day	17.4 ± 7.6 (1)	18.5 ± 3.6 (4)
	night	49.5 ± 10.6 (1)	37.1 ± 7.2 (4)
0.010	Day	59.1 ± 11.5 (4)	3.5 ± 1.3 (20)
	night	59.1 ± 8.6 (4)	77.3 ± 9.9 (20)
0.019	Day		7.0 ± 1.6 (40)
	night		25.7 ± 4.9 (40)
0.026	Day	56.8 ± 5.7 (10)	
	night	45.7 ± 4.2 (10)	
0.039	Day		5.6 ± 1.7 (80)
	night		17.3 ± 2.0 (80)
0.053	Day	140.1 ± 54.3 (20)	4.1 ± 1.2 (100)
	night	174.1 ± 40.5 (20)	8.7 ± 1.8 (100)
0.105	Day	132.8 ± 7.2 (40)	24.6 ± 3.0 (225)
	night	163.8 ± 6.7 (40)	26.1 ± 3.19 (225)

Response to Predators in Environments of Different Size

Addition of predaceous, lotic species of dace (*Rhinichthys* sp.) to the large stream tanks produced, within minutes, a significant drop in amphipod activity level ($p<0.001$, t-test; Table 5). However, this did not occur in the small stream tanks. In both sizes of tank each animal drifted several times per hour.

Discussion

Our designated categories of drift refer primarily to what is generally accepted to fall under the definition of "behavioural drift". The data may, nevertheless, contain some low-level component of "constant drift" as the latter is difficult to single out. Active and passive downstream transport were maximal, and upstream activity was minimal, at 28 cm/s. However, the overall level of activity at this speed was the lowest of any of the current regimes, agreeing with our prior finding that, in the laboratory, optimum current conditions for this species appear to be around 25 cm/s (Williams and Moore 1982). We assume that organisms move around less in conditions that they prefer but are more active in less suitable surroundings, the result of simple kinetic or taxic responses (Williams 1986). In the field, in contrast, *G. pseudolimnaeus* preferentially colonized microhabits exhibiting close to zero current rather than those in the range of 15–25 cm/s; this result may have been influenced by

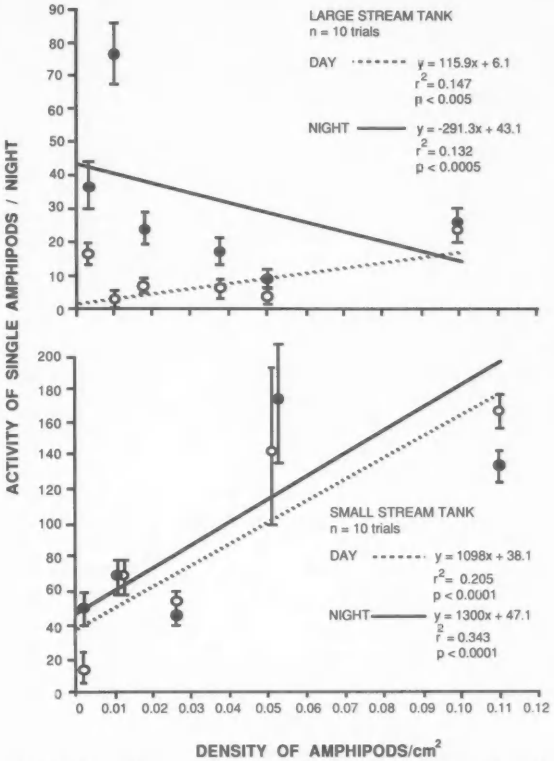


FIG. 10. Regression lines of activity level against amphipod density in the large and small stream tanks (day and night) ($n = 10$; 10 trials each consisting of 10 consecutive hours of day or night time activity at each density).

TABLE 5. Nocturnal activity response of *Gammarus pseudolimnaeus* to the presence of dace (*Rhinichthys* sp.) in large and small stream tanks, under standard tank conditions of substrate, depth and current.

Tank size	Level of activity (mean no. drifting/h ± 1SE) (*n*)		Probability (from *t*-test)
	No fish	Fish	
Small	44.7 ± 32.7 (15)	60.3 ± 45.9 (15)	>0.5
Large	115.0 ± 12.2 (9)	50.0 ± 7.6 (9)	<0.001

other environmental factors difficult to control in the field (Williams and Moore 1986).

As current speed increased to 40 cm/s, active and passive downstream transport decreased in importance while both upstream activity and overall activity levels increased substantially in the case of rough, fast current. *Gammarus pseudolimnaeus* can be found, in nature, in currents up to 55 cm/s (Rees 1972) though it tends to avoid them (Marchant and Hynes 1981). The animals forced, in the laboratory, to endure high currents, hugged the substrate and showed increased positive rheotaxis, presumably to compensate for downstream transport some of which may be due to "catastrophic" displacement. Exposure to current, measured as animals sitting on the screens under the photocell, decreased linearly with increasing current ($y = -0.401x + 24.09$; $R^2 = 0.971$; $p < 0.05$). "Erodibility" of animals, and hence entry into the drift does not appear to rise automatically with increasing exposure to current (Statzner et al. 1984) although Wiley and Kohler (1984) have proposed that any behaviour that increases the probability of either exposure to eroding currents or erosion itself, substantially increases the chances of passive entry into the drift. On the other hand, *G. pseudolimnaeus* along with some other benthic invertebrates, such as the mayfly *Baetis*, seem to be in full control of their environment and do not respond to variation in current entirely as if they were inorganic particles of sediment (Campbell 1985).

Our data revealed important diel differences in amphipod activity between darkness and light. A nocturnal peak in the frequency of activity of *Gammarus* is well documented both in the field and laboratory (e.g. Waters 1962; Wallace et al. 1975). However, the significant differences in swimming speed of individuals between day and night is intriguing. Faster swimming in the daytime (at 15 and 28 cm/s) might be interpreted as minimizing exposure to visual predators but why should this pattern be reversed at 40 cm/s (smooth flow) and at zero current? Lack of any diel difference in swimming speed at 40 cm/s (rough flow) could perhaps indicate steady, uniform swimming in an attempt to escape a totally unacceptable current regime — recall that this condition resulted in maximum overall activity levels.

In both sizes of stream tank, individual amphipods drifted significantly farther (27–31%) at night than during the day. Elliott (1971) found no difference between day and night but found that distance drifted was related to species, current, and substrate type. The greater nocturnal drift distances recorded for *Baetis* by Statzner and Mogel (1985) were thought to be the result of disorientation of the nymphs at the loss of a dorsal light stimulus. Total distances drifted by individual *G. pseudolimnaeus* in a single drift episode differed significantly between small and large stream tanks ($\bar{x} = 0.45$ and 0.59 m, respectively at night). Both estimates fall short of the field-measured range reported for *Gammarus* (e.g. $\bar{x} = 1.0$ to 5.7 m *G. pulex* (L.); Elliott (1971) and $\bar{x} = 28.5$ m *G. pseudolimnaeus*; McLay (1970)). In our small stream tanks, individual animals underwent an average of 6.8 drift episodes (Table 3) during 12 h of darkness for a total mean nightly downstream displacement of 3.04 m. Individuals in the large stream tanks underwent an average of 37.9 episodes during which they covered a mean total distance of 22.37 m. Mean distances drifted by invertebrates in a disturbance experiment in streams in British Columbia ranged from 0.58 to 13.85 m (Larkin and McKone 1985) and distances drifted by three species of mayfly in a combined model/field study in Alberta ranged from 6.43 to 14.98 m (Ciborowski 1987). Thus although our individual drift episode distances are low compared with other studies, our estimates of total nightly displacement are closer. Field studies have not shown whether individual animals undergo multiple nocturnal drift episodes. The fact that dead animals touched the walls or substrate significantly more often in the small stream tanks whereas the rate of touching by live animals was the same between tanks strongly suggests a behavioural response. Thus *G. Pseudolimnaeus* may test the substrate at regular intervals while drifting. This process appears to be independent of local environment scale.

Variance around the mean values of the drift parameters shown in Table 3 is generally low indicating considerable similarity in drift behaviour between individual animals which, perhaps, points to a more structured (in terms of time and/or distance) format to the drift process than has been thought in

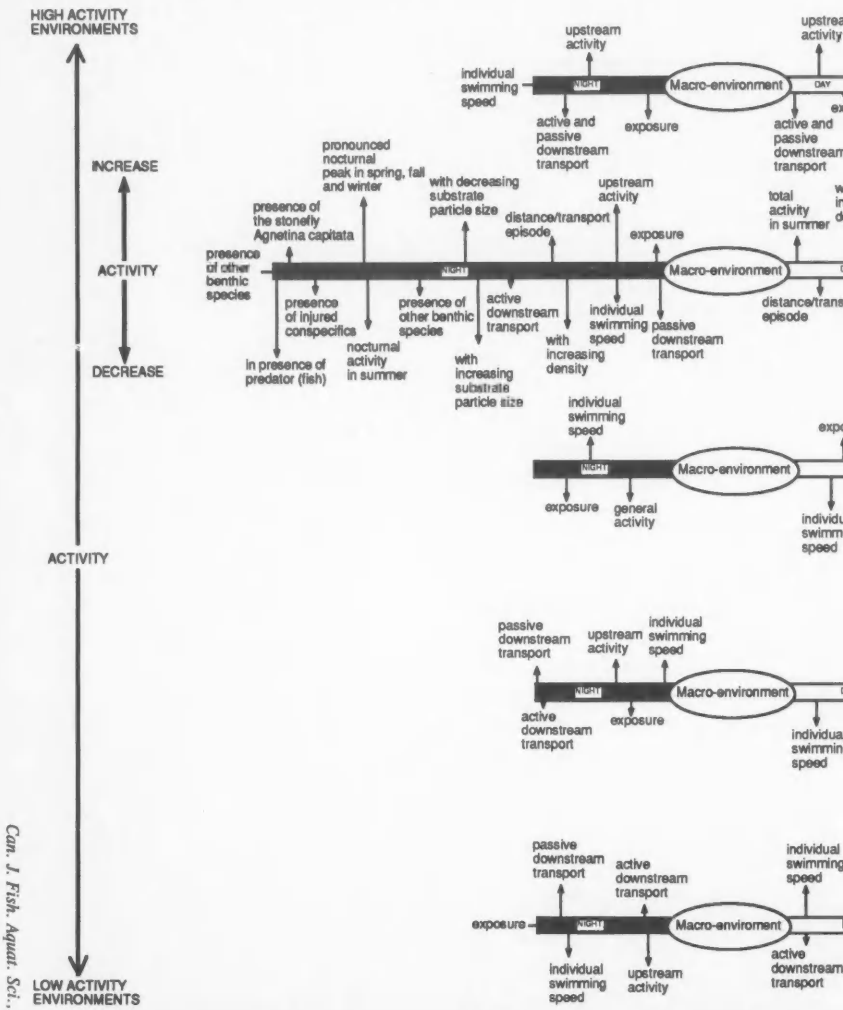
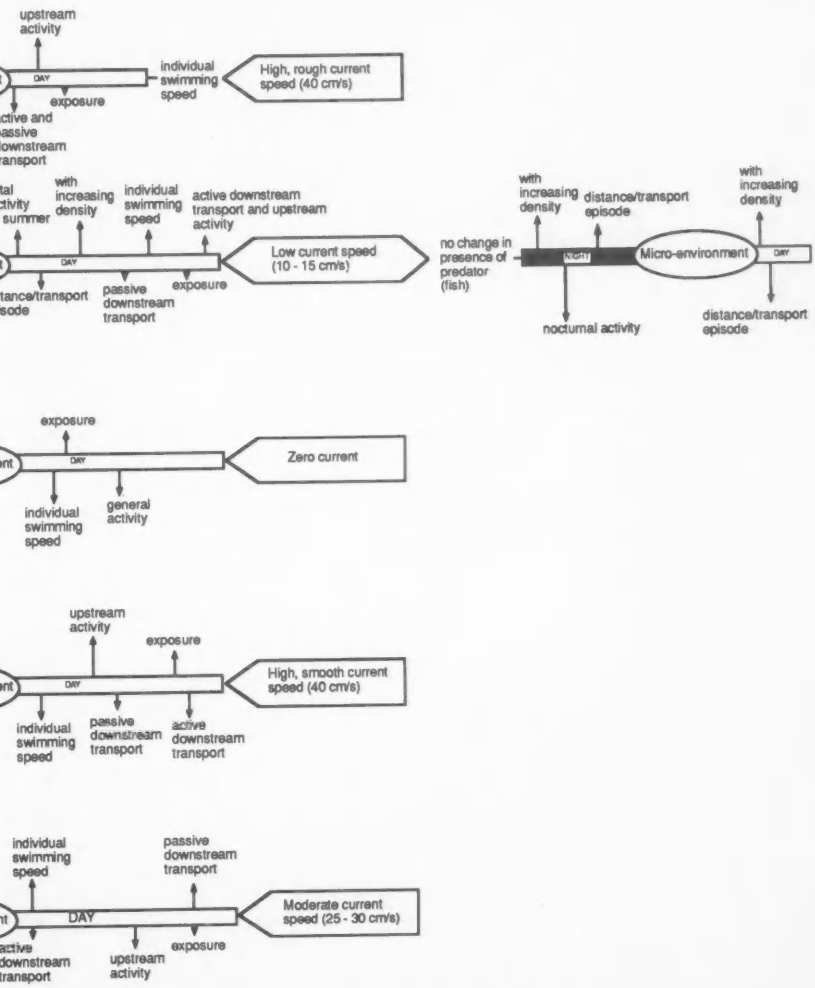


FIG. 11. Summarial schema of the typical activity responses of adult *Gammarus pseudolim- naeu* as increasing above or decreasing below the horizontal day/night bars; relative amount of change in ac based on experiments performed in the large stream tanks while "microenvironment" indicates expe the figure and decrease towards the bottom; based on data from the present study together with that f

CTIVITY LEVEL AND TYPE IN GAMMARUS PSEUDOLIMNAEUS



lim- naeus to manipulation of its environment in the laboratory (individual case activity is shown nge in activity is approximated by the lengths of the arrows; "macroenvironment" indicates data ates experiments done in the small stream tanks; overall activity levels increase towards the top of vith that from Williams and Moore 1982 and 1985).

the past. The larger variances associated with distances drifted in some previous studies may be due to the manner of creation of drift events. For example, quite a number of studies have generated drift by mechanically disturbing the benthos. Presumably there is a difference in the determination/ability of artificially-displaced individuals (compared with behavioural (= voluntary) drifters) to return to the substrate and this will affect the distance drifted. The position in the water column to which animals are relegated by disturbance also may affect the latter as, e.g. a particular species normally may drift close to the substrate but be displaced higher by experimental disturbance. An alternative explanation for the lower variance in our drift data is that, in the field, estimates include animals drifting from a number of upstream microhabitats thus the physiological or behavioural states of the animals may be more varied.

Relationships between drift densities and benthic densities have been sought, frequently, with limited success (Waters 1972; Brittain and Eikeland 1988). In one instance where density dependence was demonstrated (in the stonefly *Taeniopteryx*), the relationship broke down at current velocities less than 25 cm/s (Walton 1980). On occasion, drift of one larval group appears to be more related to the benthic densities of other larval groups than to their own (Statzner et al. 1987). No relationships have been shown between drift of various species of *Gammarus* and their own benthic densities in either field or laboratory studies (Statzner et al. 1984). Our data show a positive relationship between level of drift activity and benthic density of *G. pseudolimnaeus*, during both day and night, in the small stream tanks although the relationship possibly becomes asymptotic at high benthic densities (Fig. 10). In the large stream tanks the daytime relationship was different from that seen at night. Negative correlations, such as seen at night, have been documented for some southern Australian upland stream species (Graesser and Lake 1984).

It is known that drift rate in *G. pseudolimnaeus* varies according to microenvironmental features such as substrate size, current speed, and the presence of other members of the benthic community (Williams and Moore 1982, 1985, Fig. 11) and this has been shown for other benthic species as well (Walton et al. 1977, Williams 1986). The major difference in environmental conditions between our large and small stream tanks was one of scale. These and other differences in the various drift parameters measured between the two sizes of tank together with the loss of marked nocturnal activity in the small tanks and the differential response to predators between tanks may reflect differences in perception of local environmental scale by the amphipods. An evaluation of the streambed may be made during the periodic contacts that *G. pseudolimnaeus* makes with the substrate during the transport phase of a drift episode.

It might be argued that small stream tanks, while allowing accurate estimation of benthic densities and registering of individual drift activity, represent somewhat more artificial environments than larger versions, and thus some observed differences may be due to behavioural artifacts (Statzner et al. 1984). There does not appear, however, to be any proof to support this in the literature. Moreover, drift density is typically less in small versus large rivers (Armitage 1977; Ciborowski 1987).

Our data support the recent hypothesis of Ciborowski (1987) that "the dimensions of small streams may be such that free-ranging individuals could sample the entire range of microhabits available solely through relatively short-scale benthic movements". Although Ciborowski's (1987) proposal applied to the characteristics of populations that had been selected for, rather than to plasticity on the part of genetically similar individuals, our data suggest that it may be applicable to the latter as well. Thus, in our small stream tanks, the volume/area of local environment may have been sufficiently small so as to enable individual amphipods to retain some form of awareness of, or familiarity with, its properties. Perhaps having perceived a "safe", though finite, environment the animals abandoned the need to be primarily night active resulting in the loss of the typical diel activity pattern. Further, even in the presence of the odour of a predator, after failing to encounter a real (or more tangible) threat within their "known" environment, they either ignore or habituate to the stimulus. An alternative, though related, explanation could be that, in the small tanks, individual amphipods contact the walls of the tanks more frequently than in the larger tanks (Table 3). As the tank walls probably register as vertical rock faces, the animals' overall perception of their own status in the small tanks may be one of being in the interstices between large rocks in a complex, "safe" (= predator free) environment. This results in reduced activity (Williams and Moore 1982) and loss of response of predators. We do not mean to imply here a level of consciousness above that normally attributed to invertebrate animals but rather behavioural changes resulting from optimal responses to particular environmental stimuli.

In this study we have provided evidence of the complexity of the drifting process in running water. We conclude by combining these results with those of our previous work on *G. pseudolimnaeus* to emphasize this complexity (Fig. 11). Clearly, this species is more active in some environments than in others. However, even within a single environment, various biotic and abiotic factors act independently or interactively to control the qualitative and quantitative nature of both drift and upstream movements. The details of these relationships, shown in Fig. 11, are largely self explanatory.

Acknowledgements

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Lake Trout (*Salvelinus namaycush*) Growth Potential Predicted from Cisco (*Coregonus artedii*) Population Structure and Conductivity

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Trippel, E. A., and F. W. H. Beamish. 1989. Lake trout (*Salvelinus namaycush*) growth potential predicted from cisco (*Coregonus artedii*) population structure and conductivity. Can. J. Fish. Aquat. Sci. 46: 1531–1538.

Trophic dynamics between lake trout (*Salvelinus namaycush*) and cisco (*Coregonus artedii*) were examined in a set of 10 northwestern Ontario lakes that ranged in conductivity by nearly an order of magnitude. Diets revealed the possibility of interspecific competition for invertebrate prey prior to initiation of piscivory by lake trout at approximately 200 mm fork length (FL). Von Bertalanffy growth equations (based on otolith ages) were used to estimate time to attain this length (1.4–3.0 yr). Contrary to anticipated results, lake trout reached this size more rapidly in lakes with high cisco abundance. Presumably, this relationship was caused by improved food conditions for young trout in some of the more productive waterbodies. However, after removing the collinearity between lake conductivity and nonpiscivorous growth by regression analysis, there was no relationship between the time for lake trout to reach 200 mm and cisco abundance. Piscivorous growth varied (L_∞ = 508 to 740 mm) extensively among the 10 populations and was likely a function of growth efficiency from different food sources. Using stepwise multiple regression, 81% of the L_∞ variation among lakes was explained by cisco abundance and mean size. Linear regression between L_∞ and mean size of trout (but not trout abundance) on conductivity generated significant positive relationships.

Les relations trophiques entre le touladi (*Salvelinus namaycush*) et le cisco (*Coregonus artedii*) ont été étudiées dans dix lacs du nord-ouest de l'Ontario dont la conductivité des eaux pouvait différer par un facteur de tout près de 10. Comme l'a montré l'analyse des régimes alimentaires de ces espèces, la compétition interspécifique pour les invertébrés était possible avant que le touladi commence à se nourrir de poissons, c'est-à-dire quand sa longueur à la fourche atteint 200 mm. Les équations de croissance de Von Bertalanffy (fondées sur la détermination de l'âge à l'aide des otolithes) ont été utilisées pour évaluer le temps nécessaire au touladi pour atteindre cette longueur (1,4:–:3,0 années). Contrairement aux résultats attendus, les touladis ont atteint cette taille rapidement dans les lacs où l'abondance des ciscos était élevée. Nous pensons que cette relation est attribuable au fait que certains des lacs les plus productifs offraient aux jeunes touladis de meilleures conditions d'alimentation. Cependant, après avoir supprimé, grâce à l'analyse de la régression, la colinéarité entre la conductivité du lac et le taux de croissance des touladis avant qu'ils commencent à se nourrir de poissons, aucune relation n'est apparue entre le temps nécessaire au touladi pour atteindre une longueur de 200 mm et l'abondance du cisco. Les taux de croissance des touladis en régime piscivore variaient (L_∞ = 508 à 740 mm) largement entre les 10 populations et dépendaient probablement de la qualité des aliments consommés. L'analyse de régression multiple par degrés a révélé que 81 % de la variation de L_∞ observée d'un lac à l'autre étaient reliées à l'abondance et à la taille moyenne des ciscos. La régression linéaire nous a permis d'établir qu'il y a une relation directe significative entre L_∞ et la taille moyenne des truites, et la conductivité. Par contre, il n'y avait pas de relation significative entre l'abondance des truites et la conductivité.

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Interspecific relationships can be complex in that species typically pass through several ontogenetic feeding niches. Commonly, the young of most fish species pass through planktivory. While some maintain this foraging mode throughout their lives (Scott and Crossman 1973; Rudstam and Trapp 1986), other species advance to piscivory (Keast 1977; Jude et al. 1988). Consequently, the population dynamics of two species may be inter-related both within and between trophic levels. During early life history stages, interspecific competition may occur followed by one of the species undergoing morphological transformations which permit predation on the second species.

Examination of this type of trophic interaction is typically done within single ecosystems (Crossman 1959; Martin 1970) but is rare in lakes ranging in productivity (Donald et al. 1980; Donald and Anderson 1982). Examination of trophic dynamics along a gradient of lake productivity is of interest because of the strong relationships that aquatic abiotic conditions have with ecosystem production. For example, invertebrate forage base productivity and diversity among lentic environments is correlated with productivity (Northcote and Larkin 1956; Johnson 1974). Furthermore, aquatic productivity has long been known to influence fish community production (Northcote and Larkin 1956; Ryder 1965; Ryder et al. 1974), but in which manner abiotic productivity controls species-specific productivity and

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population attributes has only been developed for relatively few fishes (Donald et al. 1980; Mills and Chalanchuk 1987; Trippel and Harvey 1987).

The objective of this study was to examine the effects of cisco (*Coregonus artedii*) on lake trout (*Salvelinus namaycush*) growth potential across a series of lakes ranging in aquatic productivity. Ciscoes are predominantly nonpiscivorous throughout their lives (Langford 1938; Rudstam and Trapp 1986), whereas consumption of cisco by lake trout is common when the food source is available (Rawson 1961; Martin 1970; Trippel and Beamish 1987). We will (1) test for interspecific competition prior to trout attaining piscivory, (2) investigate the lake trout piscivorous growth phase in relation to cisco abundance and size and (3) examine lake trout population characteristics that vary according to lake productivity.

Methods

Ten remote northwestern Ontario lakes containing sympatric populations of lake trout and ciscoes were surveyed during summer from 1981–87 (Table 1). Lakes spanned a wide range of potential productivity based on conductivity (Table 1) which was a function of bedrock composition and surficial geology (Ryder 1964; Brousseau et al. 1985). Conductivity is correlated with other water chemistry attributes reflective of lake productivity and is highly stable (Rigler 1964; Ryder et al. 1974; Hanson and Leggett 1982). In addition, the basis for lake selection was dependent on several other criteria so as to avoid the introduction of factors irrelevant to our hypotheses. Fish species composition was similar among the ten lakes and all lakes contained *Mysis relicta*, which precluded the possibility of qualitatively different forage arrays. Lakes were lightly to moderately exploited which reduced the possibility of significant reductions in trout abundance and size characteristic of heavily exploited populations (Yaremchuk 1986; Beamish et al. 1986). The sequence in which the 10 lakes were sampled was unrelated to lake productivity.

Fish communities were surveyed during summer when diet would coincide with the fastest growth period (Fry 1937; Hanson and Cordone 1967; Martin and Olver 1980) and exclude the fasting period prior to spawning (Martin 1970). Relative abundance of the coldwater fish community in each lake was determined by fishing multifilament gillnets along the lake bottom (nine panels 7.6 m long and 2 m high each of 25, 38, 51, 64, 76, 89, 102, 114, 127 mm stretched mesh). Six of the ten lakes (Islets, Greenwich, Burnt Island, Little Joe, Loch Erne, and South Otterskin) were sampled using 68-m nets, whereas the other four (Robinson, Little Gull, Pickerel, and Greenwater) were surveyed by the Ontario Ministry of Natural Resources, Quetico-Mille Lac Fisheries Assessment Unit (QMLFAU), using 136-m multifilament gillnets of the same mesh sizes. Temperature was recorded at each net site for QMLFAU lakes. For the other lakes, bathymetric depth contours were matched to temperature profiles (Wetzel 1983). Nets were set between 1500–2100 and lifted between 1000–1500 h such that each set lasted for an average of 20 h. Locations were randomly selected from a grid pattern overlaying those sections of the bathymetric map that would permit nets to be set fully in water <12°C. Net orientation was chosen by randomly selecting one of the 16 major compass points. Choice of temperature was based on preliminary surveys and knowledge of preferred temperature of lake trout (Martin and Olver 1980). Relative abundance of lake trout and ciscoes were determined as the cumulative number of individuals captured during 400 h of fishing effort by a 68-m length of multifilament gillnet. Typically it would take 20 overnight sets to attain an adequate sample. Catches did not diminish during the 2–4 wk period required to complete each lake survey.

Intensive sampling was performed on all lake trout captured. This included fork length (± 1 mm), and removal of otoliths. Absolute age of each lake trout captured from all lakes was assessed using otoliths by the crack and burn process (Chilton and Beamish 1981). The relationship between length and age was represented for each population by the von Bertalanffy growth equation (Ricker 1975).

Stomach contents of lake trout (100–299 mm fork length (FL)) were preserved in a 4% formaldehyde solution (Trippel and Beamish 1987) for lakes Islets, Greenwich, Burnt Island, Little Joe, Loch Erne, and South Otterskin. Lake trout switched from a diet of invertebrates to one of fishes at approximately 200-mm FL in all lakes. Age at which lake trout attained this length was calculated from the von Bertalanffy equation.

Fork length was recorded for all ciscoes captured. Stomach contents of 27–175 ciscoes were collected from each of Islets, Greenwich, Burnt Island, Little Joe, and Loch Erne lakes. Food organisms were removed with forceps under a dissecting microscope and frozen in distilled water till subsequent identification. Taxa identified were fishes, crustacea, and insects. Within the

TABLE 1. Location, morphometric, and water chemistry attributes of 10 lakes. Morphometric characteristics are courtesy of the Ontario Ministry of Natural Resources. pH, alkalinity, and conductivity are mean values of four summer samles for lakes Pickerel, Robinson, Little Gull, and Greenwater. Means for the other six lakes were based on two samples. All determinations were performed within 1 d after collection by the Ontario Ministry of the Environment, Thunder Bay, Ontario.

Lake	Latitude	Longitude	Surface area (ha)	Mean depth (m)	Maximum depth (m)	pH	Alkalinity (T.I.P.)[a] (mg/L)	Conductivity (μS/cm at 25°C)
Robinson	48°11′N	91°39′W	421	12.7	35	7.01	3.57	20.7
Little Gull	49°05′N	91°36′W	326	11.3	36	7.09	5.42	23.2
Islets	49°13′N	92°16′W	189	11.4	38	7.02	5.69	24.0
Pickerel	48°37′N	91°19′W	6064	17.7	80	7.16	6.24	29.5
Greenwich	48°48′N	88°51′W	484	19.0	61	7.10	9.00	30.0
Burnt Island	48°47′N	90°51′W	110	13.7	32	7.03	9.55	38.0
Greenwater	48°34′N	90°26′W	3340	17.6	59	7.80	23.75	59.9
Little Joe	50°22′N	93°27′W	221	11.2	24	7.80	37.00	78.0
Loch Erne	48°37′N	90°21′W	1675	13.8	32	8.00	44.00	100.0
South Otterskin	49°13′N	93°38′W	213	11.8	36	8.50	86.00	172.0

[a]T.I.P. = total inflection point.

TABLE 2. Number and mean length of lake trout and ciscoes captured during 400 h of hypolimnetic fishing effort using multifilament survey gillnets. Data for lakes Robinson, Little Gull, Pickerel, and Greenwater are courtesy of the Ontario Ministry of Natural Resources.

	Lake Trout		Cisco	
Lake	Number	Mean fork length (mm)	Number	Mean fork length (mm)
Robinson	34	414	59	140
Little Gull	63	377	19	123
Islets	64	423	59	143
Pickerel	39	390	32	169
Greenwich	149	361	8	172
Burnt Island	23	406	64	155
Greenwater	75	418	122	191
Little Joe	86	490	436	135
Loch Erne	44	483	100	231
South Otterskin	51	497	237	160

crustaceans, individuals were identified according to Cladocera, Copepoda, Amphipoda, and Mysidacea. The genera *Daphnia, Bosmina* (Cladocera), *Diaptomus, Limnocalanus* (Copepoda) and one species, *Mysis relicata* (Mysidacea) were identified (Merritt and Cummins 1978). Relative contribution of each taxon to an individual's diet was assessed on the basis of freeze-dried weights.

Linear regression was employed to test whether the time required for lake trout to attain 200 mm FL ($t_{200\ mm}$) was a function of cisco abundance. The wide range in productivity in our lake set would presumably influence juvenile trout growth because conductivity is correlated with the standing stock of invertebrate forage (Northcote and Larkin 1956; Donald et al. 1980). Besides conductivity, mean lake depth also is correlated with biomass of invertebrate forage (Rawson 1955; Cullis 1986; Marshall and Ryan 1987). Consequently, the hypothesis that ciscoes slow the early growth of lake trout was tested by taking the residuals from the regression $t_{200\ mm}$ versus conductivity and regressing these against cisco relative abundance. We considered repeating the residual analysis using mean depth if it also became a significant independent correlate. To attain linearity, data were transformed into natural logarithmic values. To test if growth was density dependent we regressed age at piscivory on relative abundance of lake trout from gillnet catches. We could not obtain a more direct measure of juvenile abundance because so few small trout were captured. Influence of food particle size and abundance on lake trout maximum attainable length (L_∞) was investigated by stepwise multiple regression (SAS 1985).

Results

Cisco relative abundance varied 55-fold and mean fork length two-fold among the ten lakes (Table 2). Age at onset of piscivory ranged from 1.4–3.0 yr (Table 3).

Mysis relicta formed a large proportion of the diet of small lake trout, 100–199 mm (Fig. 1). The only other food items consumed at this size were insect larvae. Fishes were not consumed until trout attained 200 mm. Diets of small lake trout and ciscoes overlapped on *Mysis* and insect larvae. However, ciscoes also ate *Daphnia, Bosmina, Diaptomus, Limnocalanus*, several other taxa of Copepoda and amphipods. In two lakes ciscoes ate fishes young-of-the-year yellow perch (*Perca flavescens*) and slimy sculpin (*Cottus cognatus*) but the contribution made by fishes to the diet was <7% by weight. We examined the correlation between growth and conductivity (Fig. 2A) in testing the hypothesis that an increase in cisco abundance slows juvenile growth of lake trout. Indeed, without removing the effect of conductivity, it would seem that elevated cisco

TABLE 3. Time required by lake trout to attain piscivory (as represented by T_{200mm} FL) and the von Bertalanffy growth equation of 10 populations. 95% confidence limits are listed below each parameter estimate. All equations significant at $P<0.0001$.

		Parameters of the von Bertalanffy equation				
Lake	Years to attain 200 mm FL (t_{200mm})	L_∞ (FL mm)	K	t_0 (yr)	n	r^2
Robinson	3.0	598 (567–629)	0.128 (0.080–0.176)	−0.142 (−0.660–0.376)	48	0.996
Little Gull	2.2	525 (407–552)	0.206 (0.105–0.307)	−0.120 (−0.805–0.565)	67	0.992
Islets	2.7	578 (561–595)	0.157 (0.137–0.177)	−0.035 (−0.495–0.425)	100	0.990
Pickerel	2.8	596 (564–628)	0.143 (0.083–0.203)	0.036 (−0.469–0.541)	45	0.994
Greenwich	2.9	508 (466–550)	0.141 (0.081–0.201)	−0.646 (−1.469–0.177)	283	0.953
Burnt Island	2.7	610 (590–630)	0.130 (0.116–0.144)	−0.397 (−0.820–0.026)	87	0.996
Greenwater	2.0	740 (689–794)	0.109 (0.096–0.122)	−0.887 (−0.810–0.045)	189	0.982
Little Joe	1.7	619 (594–644)	0.205 (0.165–0.247)	−0.203 (−0.763–0.357)	97	0.974
Loch Erne	2.1	684 (653–715)	0.155 (0.127–0.183)	−0.088 (−0.628–0.452)	118	0.978
South Otterskin	1.4	639 (620–658)	0.229 (0.193–0.265)	−0.213 (−0.613–0.187)	91	0.984

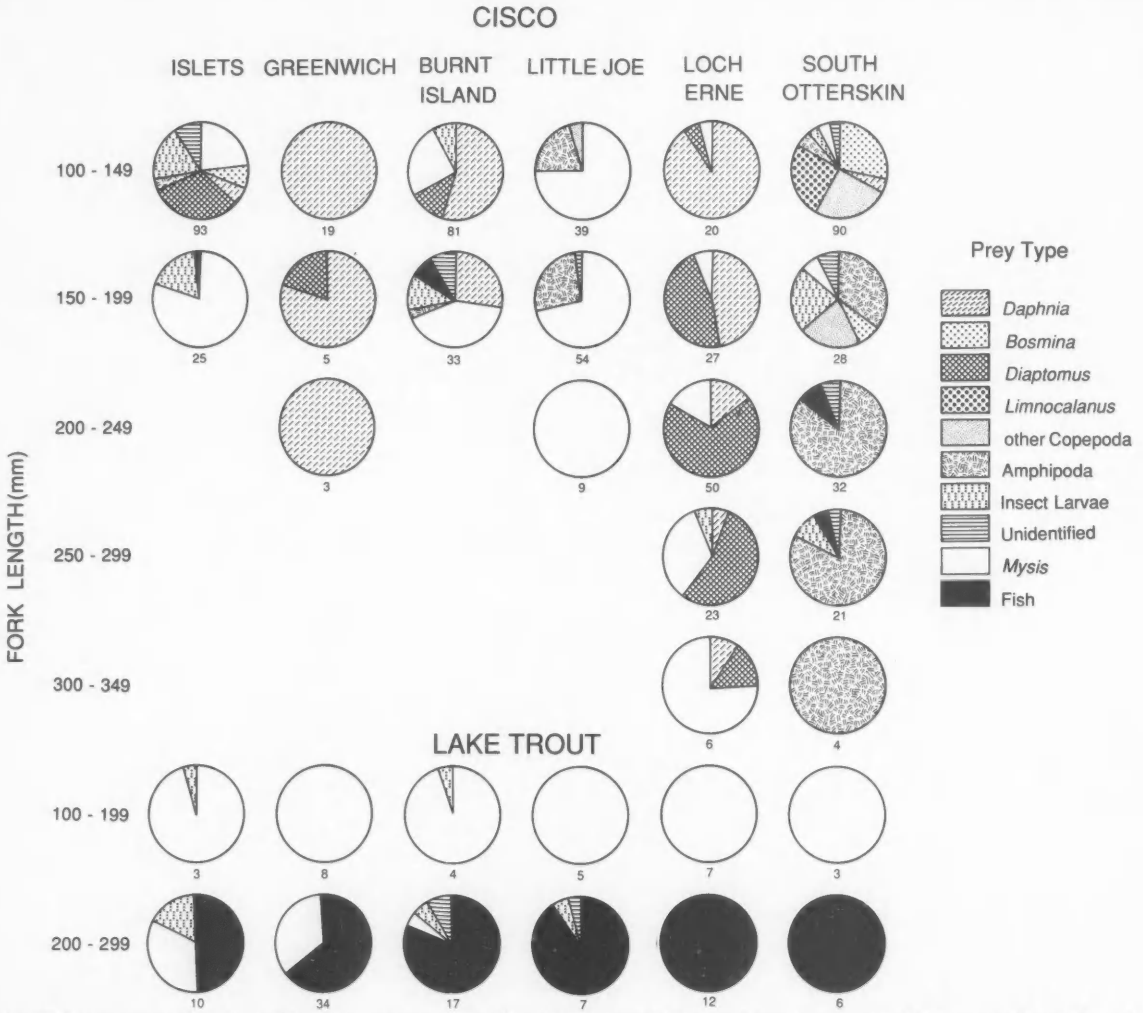

FIG. 1. Percent composition by weight of the summer diet of five size classes of ciscoes and two size classes of lake trout collected from six lakes. Results from ciscoes were calculated using freeze-dried weights and those of lake trout on preserved wet weights. Number of fish in calculations are below each figure.

abundance accelerates growth of young trout (Fig. 2B). However, after adjusting for conductivity (Fig. 2C), cisco abundance was not significantly correlated with the time required by trout to attain piscivorous size. We did not adjust for lake mean depth because it did not significantly contribute, beyond that of conductivity, in explaining variation in any of the models. Early lake trout growth was not density dependent: $\log_e$ (years to attain 200 mm FL) $= -0.09 \log_e$ (lake trout relative abundance) $+ 1.19$, $r^2 = 0.04$, $P = 0.59$.

Lake trout attained larger sizes in more productive waterbodies. Figure 3 displays the wide range in L_∞ values observed among the ten populations (508–740 mm FL) in relation to cisco relative abundance, cisco mean fork length, and conductivity. Stepwise multiple regression demonstrated that L_∞ was most strongly accounted for by cisco relative abundance which explained 53% of the variation. An additional 28% of the variation was explained by cisco mean fork length. The multivariate equation is: $\log_e (L_\infty) = 0.66 \log_e$ (cisco relative abundance) $+ 0.32 \log_e$ (cisco mean fork length) $+ 4.52$, $r^2 = 0.81$, $P = 0.003$. Conductivity predicted maximum attainable length: $\log_e (L_\infty) = 0.10 \log_e$ (conductivity) $+ 6.05$, $r^2 = 0.38$, $P < 0.05$ and mean fork length of lake trout: $\log_e (\bar{X}$ FL) $= 0.12 \log_e$ (conductivity) $+ 5.60$, $r^2 = 0.73$, $P = 0.006$. However, conductivity failed to be a significant predictor of lake trout abundance: $\log_e$ (lake trout abundance) $= 0.06 \log_e$ (conductivity) $+ 3.76$, $r^2 = 0.007$, $P = 0.82$.

Discussion

High levels of lake productivity resulted in faster growth and an earlier age of piscivory of lake trout, despite the concurrent rise in cisco abundance. Positive association between the growth of young, nonfish eating salmonids and environmental productivity also has been reported in western Canada. For rainbow

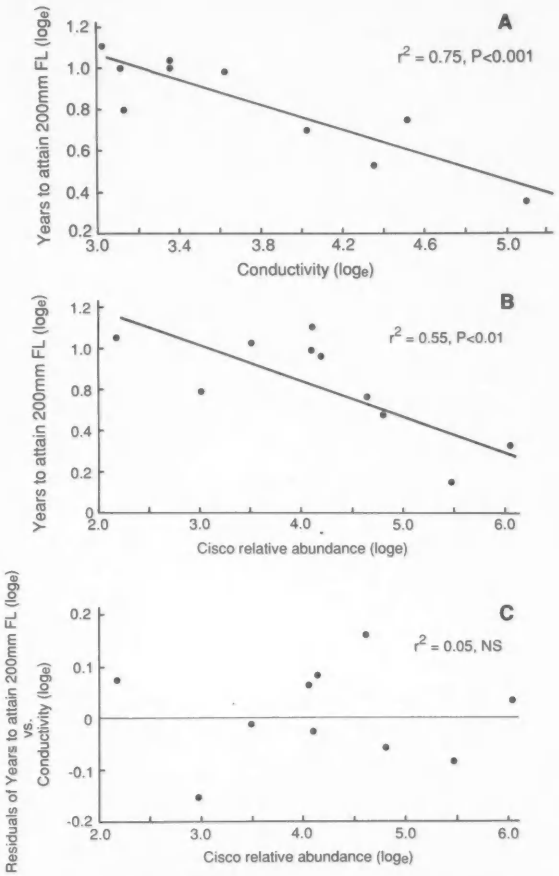
A
r^2 = 0.75, P<0.001
Years to attain 200mm FL (loge)
Conductivity (loge)
B
r^2 = 0.55, P<0.01
Years to attain 200mm FL (loge)
Cisco relative abundance (loge)
C
r^2 = 0.05, NS
Residuals of Years to attain 200mm FL (loge) vs. Conductivity (loge)
Cisco relative abundance (loge)

FIG. 2. (A) Time required for lake trout to attain 200 mm FL regressed on lake conductivity for 10 lakes: $\log_e(Y) = -0.30 \log_e(X) + 1.98$. (B) Time required for lake trout to attain 200 mm FL regressed on cisco relative abundance in the hypolimnion for 10 lakes: $\log_e(Y) = -0.16 \log_e(X) + 1.52$. (C) Regression of residuals from the relationship in Fig. 2 (A) on cisco relative abundance: $\log_e(Y) = -0.02 \log_e(X) + 0.10$.

trout (*Oncorhynchus mykiss*), 42% of the lake-to-lake variation in weight at age 2 among 23 lakes was attributed to conductivity (Donald and Anderson 1982). Similarly, for brook trout (*Salvelinus fontinalis*), weight at age 5 was positively correlated with conductivity ($r = 0.63$) (Donald et al. 1980).

Rapid growth of young lake trout in our study was likely a consequence of improved invertebrate forage regime in relation to lake productivity. The benthic standing stocks of 116 North American lakes was found by Johnson (1974) to be positively related to conductivity. A bio-index combining relative measures of plankton, bottom fauna, and fish abundance regressed in a significant positive fashion with conductivity (Northcote and Larkin 1956). Moreover, there existed a positive relationship between conductivity, benthic amphipod abundance, the relative importance of this food item in the diet of brook trout, and the trout's growth rate (Donald et al. 1980). In our study, the greater conductivity span among lakes relative to mean lake depth is the probable reason for the latter's insignificant predictive power.

Trophic dynamic relationships within a similar framework to our study have been examined for another freshwater species pair. Redside shiners (*Richardsonius balteatus*) invaded Paul Lake, British Columbia 36 yr after rainbow trout were first stocked into the barren lake (Crossman and Larkin 1959). Ontogenetic growth patterns of the trout were a function of competition for food with shiners followed by predation on shiners. Shiners drastically reduced the *Gammarus* population relative to their former abundance, such that trout, as well as the shiners, shifted their diets to other prey (Johannes and Larkin 1961). The effects of competition were manifested by a decline in the growth rate of small trout (<250 mm) (Larkin and Smith 1954); however, the foraging on shiners was marked by improved growth of large trout (Crossman 1959; Crossman and Larkin 1959).

Similarly, interspecific competition has been previously postulated between lake trout and ciscoes (Martin 1970) in a PreCambrian lake void of *Mysis* (Martin and Chapman 1965). Ciscoes were introduced into Lake Opeongo, Ontario in 1948 to serve as food for the slow-growing lake trout population (Fry 1939; Martin 1970; Martin and Fry 1973). Although mean length at age 2 decreased, body weight of lake trout remained unchanged during pre- and post-cisco introductory periods (1936–65) providing support for an absence of competition during the nonpiscivorous phase (figure 5 in Martin 1970). However, older lake trout (3–6 yr, 250–425 mm) grew less after the cisco introduction. The diet of these medium size trout was marked by a substantial reduction of young-of-the-year yellow perch. Martin (1970) speculated that the cisco introduction reduced the perch population, perhaps through interspecific competition, and thus indirectly suppressed growth of lake trout prior to their switch to a diet consisting primarily of ciscoes.

Some researchers have reported a growth depressing effect on lake trout by nonpiscivorous fishes. Powell et al. (1986) found that body condition of lake trout at age 5 in eight boreal forest lakes declined with increasing cumulative abundance of several coregonines, namely ciscoes, lake whitefish (*Coregonus clupeaformis*), and round whitefish (*Prosopium cylindraceum*) ($r = -0.80$). In four small oligotrophic lakes, there occurred an inverse relationship between the biomass of stocked lake trout subsequently recaptured and biomass of all hypolimnetic species present, mainly yellow perch, round whitefish, lake whitefish, and white sucker (*Catostomus commersoni*) (Gunn et al. 1987). Conversely, juvenile lake trout in sympatry with nine species of coregonines did not exhibit a retarded growth pattern (Eschmeyer 1957; Smith 1968). In two lakes without ciscoes, the growth of young lake trout matched the slowest rate observed in our lake set, 200 mm in 3.0 yr (Martin 1966; P. Ryan, unpubl. data).

Ciscoes seemingly are more influential on the piscivorous rather than nonpiscivorous growth phase of lake trout as revealed by the wide range in maximum attainable length among populations. Growth of fishes is highly dependent on prey size (Martin 1966; Paloheimo and Dickie 1966; Kerr 1971a,b,c). This is related to the energetic costs of foraging in relation to energy gained from each food particle digested. For example, relative growth efficiency in rainbow smelt (*Osmerus mordax*), represented by *K*-lines (Kerr and Ryder 1977), was positively correlated with size of prey consumed through the full suite of trophic level advancements from planktivory to piscivory (Evans and Loftus 1987). In fact, absence of large prey from a lake could lead to stunting in northern pike (*Esox lucius*) (Diana 1987).

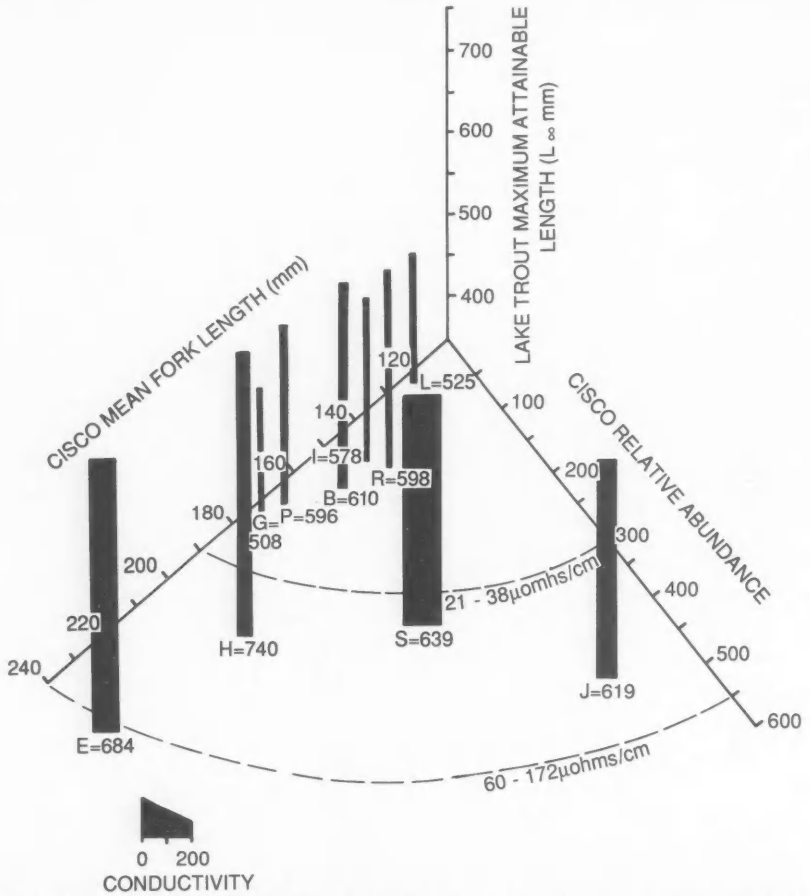

FIG. 3. Inter-relationships among the von Bertalanffy estimate of maximum attainable length of lake trout, conductivity, and estimates of cisco mean size and abundance in the hypolimnion for 10 lakes. Width of bars represent magnitude of conductivity. R = Robinson, L = Little Gull, I = Islets, P = Pickerel, G = Greenwich, B = Burnt Island, H = Greenwater, J = Little Joe, E = Loch Erne, S = South Otterskin.

Kerr (1971b) cleverly revealed the inter-relationships of food particle size and abundance with growth efficiency for lake trout. Body weight of lake trout on a plankton diet (plankton individual weights 0.001–0.01 g) did not exceed an asymptotic level of 1000 g, even when feeding on extremely high plankton densities (0.05 g/m^3). In contrast, a much larger trout mass (>3000 g) was attained when feeding on small fish (25 g) that were only 1/50th as abundant. In our study we deduced growth variability to be caused by the contrasting structure of cisco forage supplies among lakes. The main criteria for large maximum attainable length was prey abundance and secondly its mean size. Perhaps, in contrast to Martin's (1966) study which contrasted planktivores and piscivores, prey size variation in our study was not as expansive consequently the greater dependence on prey abundance.

Based on the research of other coldwater teleosts, we would have expected density of lake trout to have been an increasing function of lake productivity. For example, for arctic charr (*Salvelinus alpinus*) and lake whitefish moderate increases in lake productivity associated with whole-lake fertilization led to enhanced survival during the first year of life and consequently increased population density (Langeland 1982; Mills and Chalanchuk 1987). Lack of increased abundance of lake trout with increased productivity in our study may be due to predation on young-of-the-year larval trout by ciscoes under the ice or consumption of spawned trout eggs. To our knowledge, no study exists concerning the early spring diet of ciscoes. Our summer examination revealed they are capable of consuming small fishes, though only large ciscoes possessed this capability. Interestingly, large ciscoes were more abundant in the more productive ecosystems and combined with their overall higher abundance, ciscoes could possibly limit trout recruitment through predation.

Our findings suggest that prediction of trophy lake trout fisheries and mean size of fish by conductivity, is conceivable from limited lake survey data on lightly to moderately exploited systems containing cisco. Stocking of lake trout is a successful method of initiating naturally reproducing populations in inland lakes (Olver and Lewis 1977; Hitchins and Samis 1986). However, sizes of fish reared for stocking often vary among hatcheries and even within hatcheries. Because growth of young trout is most rapid in productive lakes, perhaps to offset this non-

uniformity in size, a management strategy may be to stock smaller individuals in more productive waterbodies. Lastly, it should be noted that our predictive equations were developed on a somewhat restrictive set of lake characteristics, readers should be cautioned that the equations are not recommended for widespread, unconditional application.

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Among-Population Variability of Fish Growth: III. Influence of Fish Community[1]

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Boisclair, D., and W. C. Leggett. 1989. Among-population variability of fish growth: III. Influence of fish community. Can. J. Fish. Aquat. Sci. 46: 1539–1550.

We assessed the relationship between in situ fish growth and fish community descriptors in 12 yellow perch (*Perca flavescens*) populations that exhibited a 1.8 to 10-fold range in growth rates depending on age class. Data on the quantity and quality of food consumed were used to assess the mechanisms by which fish community composition influences in situ growth rates. Among-population variability in growth rates of the 12 perch populations was most strongly and consistently explained by the average density of the total fish community and/or the average density of cyprinids. A multivariate model involving fish average density and perch feeding levels explained 90% of the variance in perch growth. Perch growth rates decreased as fish average density increased ($r^2 = 0.60$) and increased as feeding levels increased ($r^2 = 0.30$). We found no significant relationship between the quantity of food consumed by perch and fish average density. The percent contribution of prey taxonomic groups to perch diet was not related to fish average density. We suggest that nonexploitative interactions (operating through increased activity costs) provides a more credible explanation for the negative relationship between perch growth and fish average density than does exploitative competition (decreased total quantities of food consumed or prey quality).

Nous avons évalué la relation entre la croissance in situ des poissons et une série de descripteurs de la communauté de poissons pour 12 populations de perchaudes (*Perca flavescens*) dont le taux de croissance varie par un facteur de 1,8 à 10 selon la classe d'âge. Nous utilisons des données déjà publiées sur la quantité et la qualité de la nourriture consommée pour évaluer le (s) mécanisme (s) par le(s)quel(s) la composition de la communauté de poissons influence la croissance in situ des poissons. La variabilité inter-population de la croissance des 12 populations de perchaudes a été le plus fortement et régulièrement expliquée par la densité moyenne de la communauté de poissons et/ ou la densité moyenne de cyprinidés. Un modèle multivarié utilisant la densité moyenne de poissons et la quantité de nourriture consommé a expliqué 90 % de la variance de la croissance. La croissance des perchaudes a toujours diminué avec la densité moyenne de poissons ($r^2 = 0,60$) et augmenté avec la quantité de nourriture consommée ($r^2 = 0,30$). Nous n'avons pas trouvé de relation significative entre la quantité de nourriture consommée par les perchaudes et la densité moyenne de poissons. La contribution des groupes taxonomiques de proies à la diète des perchaudes n'a pas été significativement relié à la densité moyenne des poissons. Nous suggérons que les interactions non-exploitantes (opérant par une augmentation du taux d'activité) explique plus adéquatement la relation négative entre la croissance des perchaudes et la densité moyenne des poissons que la compétition d'exploitation (diminution la quantité totale de nourriture consommée ou la qualité des proies).

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The relationship between fish growth and fish density (number of fish per square metre or biomass) has long been recognized (Petersen 1894; Dahl 1917). Fish communities, especially at high densities, are known to affect quantitatively and qualitatively their prey communities (Hayne and Ball 1956; Hrbacek et al. 1961; Hrbacek 1962; Brooks and Dodson 1965; Mittelbach 1981, 1983; Ciepielewski 1985; O'Neil and Hyatt 1987). The presence of superior competitors and/or intra-specific competition have also been shown to influence fish growth (Lammens et al. 1985; Hanson and Leggett 1985; Rose 1986; Persson 1986, 1987; Holt and Kotler 1987; Mettelbach 1988; also see Schoener 1983 for a review of earlier works).

The negative relationship between fish growth and fish density is hypothesized to occur primarily via exploitative competition which decreases the average quantity and quality of the food consumed by individual fishes as fish density increases (Alm 1946; LeCren 1958; MacLean and Magnuson 1977; Peterman 1984; Henderson 1985; Henderson and Brown 1985; Hansson 1985; Hanson and Leggett 1986; Persson 1986, 1987).

In this paper we examine the power of fish community descriptors to explain among-population variability in in situ fish growth rates. We also draw on previously published data (Boisclair and Leggett 1989a,b) on the quantity and quality of food consumed by these populations to assess the mechanisms

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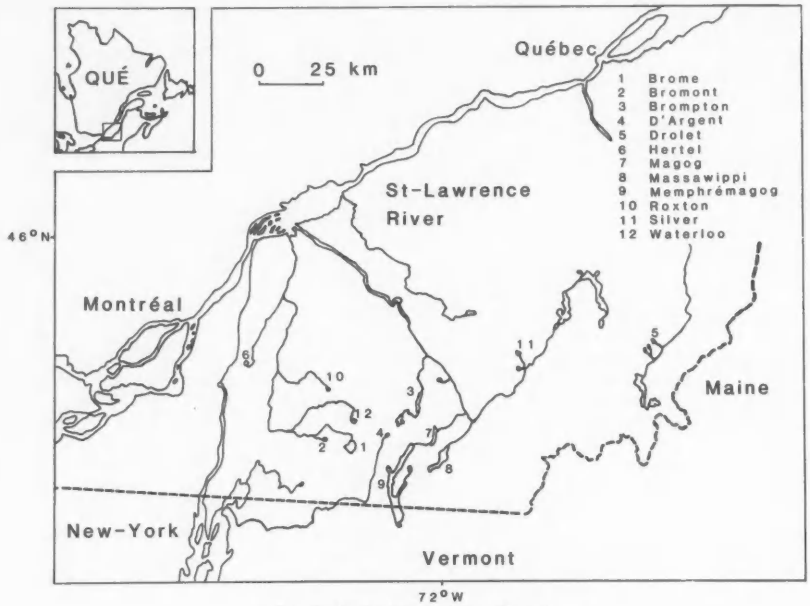

FIG. 1. Study area and sampling sites.

by which fish community composition influences in situ growth rates.

Methodology

Species and Populations Studied

During 1984 we studied yellow perch (*Perca flavescens*) populations resident in the littoral zones of 12 lakes of the Eastern Townships region of Quebec (Fig. 1). These populations exhibited a range of growth rates that approached the full range reported for perch at this latitude (Grimaldi and Leduc 1973; Nakashima and Leggett 1975; Heath and Roff 1987; Boisclair and Leggett 1989a). The morphological and limnological characteristics of the lakes surveyed are described in Rasmussen (1988a,b) and Boisclair and Leggett (1989a).

Sampling

Quantitative description of the 12 fish communities in the littoral zones of these lakes was carried out coincident with our analysis of the relationship between fish growth rates, food consumption, and diet composition in the yellow perch (Boisclair and Leggett 1989a,b). Growth rates (RGR = grams wet per grams wet per day) were estimated for each of three age classes (I+, II+, III+) in each population as:

$$(1)\quad \mathrm{RGR} = \frac{W_1 - W_f}{J_1 - J_f} \cdot W_m^{-1}$$

where W_f and W_1 are respectively mean fish weights at the first (J_f) and last (J_1) Julian date of the sampling season (i.e. late May to late September 1985). W_m is the mean fish weight during the interval $J_1 - J_f$ (Boisclair and Leggett 1989a). The quantity of food consumed by perch of any given population and age class (grams dry per grams wet per day) was estimated by combining field derived values of digestive tract contents and evacuation rates (Boisclair and Leggett 1989a). The growth efficiency for each combination of perch age class and population was defined as average growth rates expressed as percentages of average food consumption rates (Boisclair and Leggett 1989a). Perch diet was described using stomach contents analysis performed on individuals belonging to each combination of perch age class and population (Boisclair and Leggett 1989b). Data were sufficient to permit analysis of the growth rates of I+ perch from the littoral zone of eight lakes, and II+ and III+ perch from 10 populations (Boisclair and Leggett 1989a). Growth rates in the populations sampled varied by 1.8 (age I+ fish) to 10-fold (age II+ fish; Table 1).

Between the months of July to September 1985, four seine hauls were executed in each lake to define their littoral fish communities. In the study area, the littoral zone of lakes can be defined as the region extending from shore to the 5-m depth isobath (Boisclair and Leggett 1985). A 50 m × 3 m (0.6-cm^2 mesh) knotless nylon bag seine was deployed to fully enclose an area of 460 m^2. All sampled fish >50 mm total length were identified, measured (±1 mm total length (TL)) and weighed with an electronic balance (±0.1 g wet) within 4 h of capture. Fish ≤50 mm TL were not adequately sampled by our seine and were thus discarded even when accidently captured.

Description of the Fish Communities

The term "average density" (numbers per square metre) is used throughout this paper to describe the average number of fish captured by our seine per unit area of littoral zone sampled. Moreover, the term "average biomass" (grams wet per square metre) is used to describe the average weight of fish captured by our seine per unit area of littoral zone sampled. These two descriptors of the littoral zone fish community (C_j) were estimated for each fish species j in the littoral zone of each lake as:

TABLE 1. Relative growth rate (RGR; grams wet per grams wet per day) and growth efficiency (K_1; percent) for each combination of perch age class and population studied ($A \cdot P$; Boisclair and Leggett 1989a).

$A \cdot P$	RGR	K_1
Memphremagog I	0.014	24.5
Silver I	0.014	23.0
Drolet I	0.013	21.2
Massawippi I	0.013	13.9
Brompton I	0.010	16.1
Waterloo I	0.010	47.3
D'Argent I	0.009	25.3
Bromont I	0.008	27.6
Silver II	0.010	16.1
Magog II	0.009	12.9
Memphremagog II	0.008	12.9
Brompton II	0.007	10.4
Roxton II	0.006	10.2
Waterloo II	0.004	16.8
Hertel II	0.003	4.2
Bromont II	0.003	9.7
Massawippi II	0.002	2.3
D'Argent II	0.001	3.5
Waterloo III	0.006	29.2
Memphremagog III	0.005	8.2
Drolet III	0.004	6.5
Roxton III	0.004	6.7
Magog III	0.004	4.9
Brompton III	0.003	4.5
Brome III	0.002	2.2
D'Argent III	0.002	5.6
Hertel III	0.002	2.8
Bromont III	0.002	5.5

$$(2)\quad C_j = \frac{\sum_{i=1}^{4} c_{ij}}{1840}$$

where c_{ij} is the total number or the total weight of fish of species j collected during day i, and 1840 is the total littoral zone area sampled per lake ($4 \times 460\ m^2$). Average densities and biomass therefore represent an average level of potential interactions between perch of a particular age class and given fish species.

Fish community diversity in the littoral zone was estimated in each lake using the Shannon–Weaver diversity index (H; Legendre and Legendre 1979):

$$(3)\quad H = -\sum_{j=1}^{J} p_j \cdot \log_{10} p_j$$

where p_j is the percent contribution of species j to the fish community of the littoral zone of a given lake. This index was calculated on both a numerical and a body weight basis. The Shannon–Weaver index has a minimum value of 0 (communities composed of only one fish species) and a maximum value of 1 (communities composed of an equal proportion of several fish species).

The fish species identified (Table 2) were further combined into three functional groups according to the similarity of their potential to influence perch growth rates. These functional groups were characterized as the average density, and the average biomass of: (1) the total fish community (all species combined), (2) the cyprinids which are primarily planktivorous in habit (johnny darter, *Etheostoma olmstedi*; banded killifish, *Fundulus diaphanus*; silvery minnow, *Hybognathus nuchalis*; common shiner, *Notropis cornutus*; golden shiner, *Notemigonus crysoleucas*; mimic shiner, *Notropis vollucellus*; bluntnose minnow, *Pimephales notatus*; fathead minnow, *Pimephales promelas*; creek chub, *Semotilus atromaculatus*; fall fish, *Semotilus corporalis*), and (3) the piscivorous fish (northern pike, *Esox lucius*; chain pickerel, *Esox niger*; smallmouth bass, *Micropterus dolomieu*; largemouth bass, *Micropterus salmoides*; yellow perch). Only individuals >100 g wet weight were defined as piscivores because smaller individuals of these species are known to be omnivorous.

TABLE 2. Fish species sampled and abbreviations used in the text.

Scientific name	Common name	Abbreviation
Ambloplites rupestris	Rock bass	AMRU
Castostomus commersoni	White sucker	CACO
Esox lucius[a]	Northern pike	ESLU
Esox niger[a]	Chain pickerel	ESNI
Etheostoma olmstedi[b]	Johnny darter	ETOL
Fundulus diaphanus[b]	Banded killifish	FUDI
Hybognathus nuchalis[b]	Silvery minnow	HYNU
Ictalurus nebulosus	Brown bullhead	ICNE
Lepomis gibbosus	Pumpkinseed sunfish	LEGI
Micropterus dolomieu[a]	Smallmouth bass	MIDO
Micropterus salmoides[a]	Largemouth bass	MISA
Moxostoma valenciennesi	Greater redhorse	MOVA
Notropis cornutus[b]	Common shiner	NOCO
Notemigonus crysoleucas[b]	Golden shiner	NOCR
Notropis volucellus[b]	Mimic shiner	NOVO
Perca flavescens[a]	Yellow perch	PEFL
Pimephales notatus[b]	Bluntnose minnow	PINO
Pimephales promelas[b]	Fathead minnow	PIPR
Pomoxis nigromaculatus	Black crappie	PONI
Semolitus atromaculatus[b]	Creek chub	SEAT
Semotilus corporalis[b]	Fall fish	SECO

[a]Individuals larger than 100 g wet were classified as piscivorous fish.
[b]Classified as cyprinids.

Relationship between Growth Rates and Fish Community Descriptors

The relationships between perch growth rates and the average density and average biomass of individual fish species were determined for each perch age class independently by regression analysis. We similarily examined the relationship between perch growth rates by age classes and the average density and average biomass of the functional groups defined above. To qualify as an independent variable, we required that a given fish species or functional group occur in the littoral zone of >50% of lakes sampled, and comprise >10% of the fish community average density or average biomass. The quantity of food consumed by perch (Boisclair and Leggett 1989a) and a series of diet descriptors for them (Boisclair and Leggett 1989b) were also used as independent variables in some analyses. In these cases we used multiple and stepwise multiple regression techniques. The diet descriptors used as independent variables were the mean prey weight and the percent contribution of the prey taxonomic groups that occurred in the diet of >50% of the populations sampled, and comprised >10% of perch diet.

Given the large number of independent variables in these analyses relative to the number of dependent variables, we constrained the statistical procedures to include only models that involved no more than two independent variables. We used only

TABLE 3. Fish species found in the littoral zone of each lake studied, expressed in terms of richness (percentage of fish species sampled that contributed to fish community) and maximum contribution to littoral zone fish communities (fish species concerned appear in parentheses). Fish numerical and biomass diversity indices are also presented. Refer to Table 2 for the definition of fish species.

Lake	Richness (%)	Maximum contribution (%)		Diversity (0–1)	
		Number	Biomass	Number	Biomass
Memphremagog	66.7	55.9 (LEGI)	49.6 (PEFL)	0.57	0.54
Brome	57.1	51.4 (PEFL)	79.4 (PEFL)	0.50	0.34
Bromont	52.4	50.5 (LEGI)	50.0 (PEFL)	0.71	0.68
Roxton	52.4	60.3 (PEFL)	48.5 (PEFL)	0.49	0.58
Brompton	47.6	46.8 (PEFL)	33.8 (LEGI)	0.59	0.72
D'Argent	47.6	31.1 (PEFL)	35.9 (PEFL)	0.74	0.79
Massawippi	47.6	30.8 (LEGI)	58.2 (MOVA)	0.71	0.55
Hertel	33.3	56.1 (LEGI)	37.9 (LEGI)	0.49	0.64
Magog	33.3	35.8 (PEFL)	40.2 (LEGI)	0.62	0.58
Waterloo	33.3	73.4 (PEFL)	61.0 (PEFL)	0.42	0.54
Drolet	23.8	70.8 (PEFL)	69.2 (PEFL)	0.32	0.29
Silver	19.0	78.9 (PEFL)	78.9 (PEFL)	0.30	0.30

relative growth (grams wet per grams wet per day) and relative consumption rates (grams dry per grams wet per day) in these analyses. This was done for consistency with previous studies, and to preclude spurious relationships resulting exclusively from the covariations of growth and food consumption rates with fish size (Boisclair and Leggett 1989a). Analyses were performed using untransformed data, natural logarithms, and squared values. Given the total number of relationships examined, some significant models are likely to have occurred by chance. A more conservative significance level (estimated using the Bonferroni method for multiple tests, Cooper 1968; Miller 1977; Oden 1984) would be 0.0005. Because of the exploratory nature of this study we adopted the less conservative approach ($p<0.05$). The more rigorous standard, while eliminating some relationships, does not alter the broad conclusions we draw.

Relationship between Growth Efficiency and Fish Community Descriptors

The relationships between growth efficiency and fish community descriptors were examined using the same analytical procedure employed for growth rates. In these analyses absolute (grams dry per day) rather than relative consumption rates were used (Paloheimo and Dickie 1966; Boisclair and Leggett 1989a).

Growth efficiency estimates for Lake Waterloo were suspiciously high (Boisclair and Leggett 1989a; Table 1). We therefore performed analyses of the contribution of fish community descriptors to the explained variance in growth efficiency with and without data from that lake. Although the exclusion of Lake Waterloo did change the statistics of the models, it did not influence the type of relationships observed, or our interpretation of the results.

Results

Description of the Fish Communities

A total of 7773 fish distributed among 21 species occupying the littoral zone were identified, measured, and weighed (Table 2). The number of species found in the littoral zone of a given lake (Table 3) ranged from seven (Lakes Hertel, Magog, and Waterloo) to 14 (Lake Memphremagog). Yellow perch were found in the littoral zone of all the lakes studied. Golden shiner occurred in the littoral zone of 11 of the 12 lakes. White sucker (*Catostomus commersoni*), brown bullhead (*Ictalurus nebulosus*), and pumpkinseed sunfish (Lepomis gibbosus) occurred in 10 of them. Eight of the species sampled occurred in only one or two lakes. These included northern pike, silvery minnow, largemouth bass, greater redhorse (*Moxostoma valenciennesi*), common shiner, fathead minnow, black crappie (*Pomoxis nigromaculatus*), and creek chub (*Semotilus atromaculatus*) (Table 4).

With the exception of Lake Memphremagog, none of the lakes we studied had previously been examined with respect to the composition of their summer littoral zone fish community. Gascon and Leggett (1977), in their extensive description of the Lake Memphremagog fish community, reported that 16 fish species commonly inhabited the littoral zone. We recorded 14 littoral zone species in our study. The two species we did not observe were the fall fish and the rainbow smelt (*Osmerus mordax*). These species are, however, generally classified as occasional littoral zone residents. The rainbow smelt in particular, is known as a pelagic species (Scott and Crossman 1973; Gascon and Leggett 1977). We concluded that our sampling resulted in a broadly representative index of the fish species occurring in the littoral zone of the lakes studied during the summer growing season.

Fish Species Average Density

Yellow perch, pumpkinseed sunfish, and golden shiners were the most abundant species on a numerical basis (Table 3). All other species generally occurred at densities <0.05 fish$\cdot$m^{-2} (Fig. 2) and contributed $<5\%$ of the community measured by average density (Table 4; Fig. 2). Species diversity, on a numerical basis, ranged from 0.30 (Lake Silver) to 0.74 (Lake D'Argent; Table 3).

Fish Species Average Biomass

With one exception, yellow perch and pumpkinseed sunfish were the most important contributors to community average biomass (Table 3; Fig. 3). In the exception, Lake Massawippi community average biomass was composed primarily of greater redhorse (Table 3). This species was apparently absent from the littoral zone of all other lakes. In all cases, the combined average biomass of the species other than the dominants was gen-

TABLE 4. Contribution of fish species to the littoral zone fish communities of the lake studied. Occurrence is the percentage of lakes in which a given fish species contributed to the littoral zone fish community. Maximum and mean contribution are respectively the maximum and average percent contribution of a given fish species to littoral zone fish community average density or biomass (lakes concerned appear in parentheses). Refer to Table 2 for the definition of fish species.

Species	Occurrence (%)	Maximum contribution (%)		Mean contribution (%)	
		Number	Biomass	Number	Biomass
PEFL	100	78.9 (Silver)	79.4 (Brome)	43.2	43.7
LEGI	83.3	56.1 (Hertel)	50.0 (Bromont)	23.3	20.3
NOCR	91.7	28.0 (Massa.)	27.8 (Roxton)	13.2	7.1
CACO	83.3	26.1 (Drolet)	29.6 (Drolet)	3.6	8.4
SECO	58.3	25.4 (D'Arg.)	9.0 (D'Arg.)	3.2	0.9
FUDI	25.0	34.6 (Brome)	9.4 (Brome)	3.1	0.8
ESNI	75.0	14.0 (Silver)	14.2 (Silver)	2.4	3.6
ETOL	41.7	24.4 (Massa.)	1.7 (Massa.)	2.3	0.2
ICNE	83.3	7.5 (Water.)	19.2 (Bromp.)	2.2	6.3
AMRU	50.0	6.8 (Memph.)	4.5 (Silver)	1.3	1.0
MIDO	58.3	2.9 (Magog)	3.4 (Roxton)	0.7	0.8
PINO	41.7	4.1 (Massa.)	0.4 (Massa.)	0.5	0.1
MOVA	8.3	3.0 (Massa.)	58.2 (Massa.)	0.3	4.9
NOCO	8.3	2.0 (D'Arg.)	0.9 (D'Arg.)	0.2	0.1
HYNU	16.7	2.1 (Brome)	<0.1 (Memph.)	0.2	<0.1
ESLU	8.3	1.1 (Hertel)	21.5 (Hertel)	0.1	1.8
NOVO	25.0	0.5 (Massa.)	<0.1 (Massa.)	0.1	<0.1
PONI	16.7	0.7 (Roxton)	0.1 (Bromont)	<0.1	<0.1
SEAT	8.3	0.3 (Bromp.)	0.1 (Bromp.)	<0.1	<0.1
MISA	8.3	0.2 (Memph.)	<0.1 (Memph.)	<0.1	<0.1
PIPR	8.3	0.1 (Brome)	<0.1 (Brome)	<0.1	<0.1

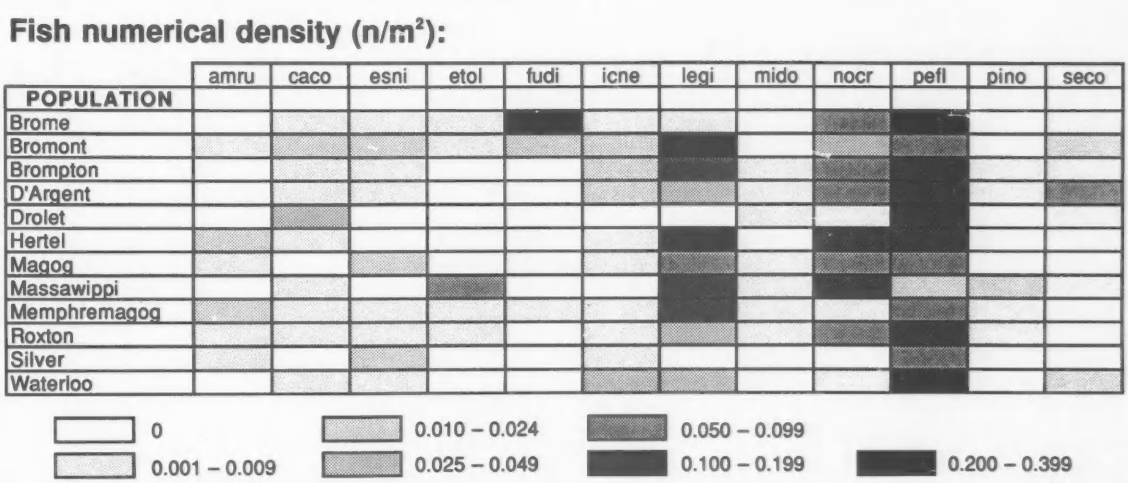

FIG. 2. Average densities (individuals per square metre) of fish species that occurred in the littoral zone of more than two lakes. Refer to Table 2 for the definition of fish species.

erally <1.0 g wet·m^{-2} (Fig. 3) and contributed <10% to community average biomass (Table 4). Species diversity, on a biomass basis, ranged from 0.29 (Lake Drolet) to 0.79 (Lake D'Argent; Table 3).

Average Density of Functional Groups

The average density of the total fish community (individuals per square metre) ranged from 0.11 (Lake Silver) to 0.75 (Lake Hertel). Cyprinids were absent from Lake Silver and had a maximum average density of 0.3 individuals·m^{-2} in Lake Brome. There were <0.010 piscivorous fish·m^{-2} in all the lakes but Drolet and Silver (0.02 piscivores·m^{-2}; Table 5).

Average Biomass of Functional Groups

Total fish community average biomass ranged from 4.07 (Lake Silver) to 12.22 g wet·m^{-2} (Lake Massawippi). Cyprinids were absent from Lake Silver and had a maximum average biomass of 2.4 g wet·m^{-2} (Lake Roxton). Piscivorous fish average biomass ranged from 0.06 (Lake Massawippi) to 2.02 g wet·m^{-2} (Lake Drolet; Table 5).

Relationship between Perch Growth Rates and Fish Species

The average density of only one of the 21 fish species sampled contributed significantly to the among-population varia-

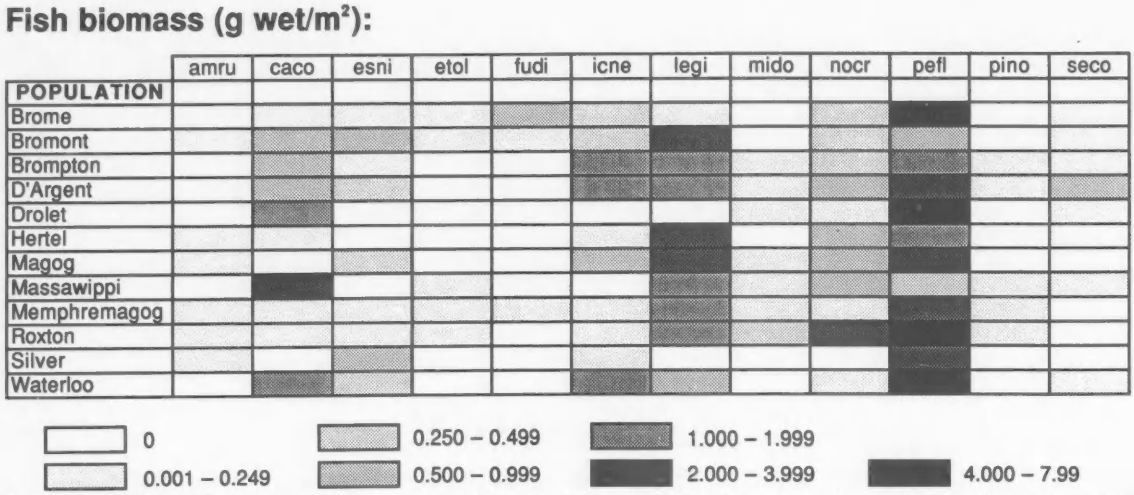

FIG. 3. Average biomass (grams wet per square metre) of fish species that occurred in the littoral zone of more than two lakes. Refer to Table 2 for the definition of fish species.

TABLE 5. Average density (*N*; individuals per square metre) and average biomass (*B*; grams wet per square metre) of fish functional groups.

	Total community		Cyprinid		Piscivorous fish	
Lake	*N*	*B*	*N*	*B*	*N*	*B*
Hertel	0.75	5.36	0.14	0.52	0.003	1.05
Brome	0.65	7.10	0.30	1.11	0.002	0.26
Bromont	0.43	7.68	0.08	0.48	0.003	0.48
Massawippi	0.39	12.22	0.22	1.24	0.0005	0.06
D'Argent	0.35	7.79	0.18	2.12	0.004	0.54
Brompton	0.35	5.77	0.06	0.43	0.002	0.45
Waterloo	0.31	10.47	0.02	0.28	0.003	0.58
Roxton	0.28	8.61	0.07	2.40	0.002	0.26
Magog	0.24	9.19	0.05	0.81	0.005	0.61
Drolet	0.14	6.66	0.004	0.07	0.02	2.02
Memphremagog	0.24	4.78	0.01	0.03	0.002	0.24
Silver	0.11	4.07	0.00	0.00	0.02	1.90

tion in perch growth rates. Despite their similar relative range of values (Figs. 2 and 3), no average biomass estimate explained a significant proportion of among-population variability in perch growth rates. Golden shiner average density explained 51% of the variation evident in growth rates of age III+ perch ($F_{1,8}=8.32$; $p<0.02$). Perch growth rates decreased as golden shiner average density increased.

Addition of the quantity of food consumed by perch (Boisclair and Leggett 1989a) or diet descriptors as variables in models relating growth rates to fish species average density or average biomass revealed no new relationships.

Relationship Between Perch Growth Rates and Fish Community Functional Groups

The most consistent and efficient univariate models relating perch growth rates to fish community descriptors involved total fish average density and cyprinid average density as variables. Perch growth rates decreased as fish average density increased (Table 6). Functional groups biomass estimates did not explain a significant proportion of among-population variability in perch growth rates. This might be related to the smaller relative range of values observed for the functional groups biomass (Table 5).

The relationships between perch growth rates and total fish and cyprinid average density were not independent (Fig. 4). Community average density increased linearly with cyprinid average density (excluding Lake Hertel; $F_{1,9}=22.91$; $p<0.001$; $r^2=0.72$).

The average density of the total fish community explained 57%, 42 and 44% of the among-population variability in growth rates of age I+, II+, and III+ perch, respectively (Fig. 5). Cyprinid average density explained 67 and 46% of the among-population variability of the growth rates of age II+ and III+ perch, respectively (Fig. 6). Cyprinid average density alone did not explain a significant fraction of growth variability for age I+ perch ($F_{1,6}=0.80$; $p>0.40$).

The best multivariate models to explain the variability of perch growth rates incorporated total fish community, or cyprinid average density, with the quantity of food consumed (from Boisclair and Leggett 1989a; Table 6). Perch growth rates were negatively related to fish average density but positively related to perch feeding levels. The average density of the total fish community ($r^2=0.56$) when combined with the quantity of food consumed ($r^2=0.31$) explained 87% of the observed among-population variability in the growth rates of age I+ perch. Cyprinid average density ($r^2=0.67$), when combined with the quantity of food consumed ($r^2=0.30$), explained 97% of interpopulation growth rates differences for age II+ perch. By itself, the quantity of food consumed was never significantly related to the average density of the total fish community or of cyprinids (Table 7). Food quantity did not significantly improve the fit of the model for age III+ perch ($p>0.15$). For that age class, the best model combined cyprinid average density and the percent contribution of Odonata to perch diet (Table 6). The percent contribution of Odonata to the diet of age III+ perch was not significantly related to cyprinid average density ($F_{1,8}=0.08$; $p>0.75$; $r^2=0.01$).

Relationship between Growth Efficiency and Fish Species

Among-population variability in perch growth efficiency was apparently related only to the average biomass of yellow perch

TABLE 6. Significant relationships ($p<0.05$) observed between (a) growth rates (RGR) and fish community functional groups (TN = total community average density; CN = cyprinid average density) and (b) between growth rates, fish community functional groups, quantity of food consumed (RDR; Boisclair and Leggett 1989a), and diet descriptors (Boisclair and Leggett 1989b). DIP and ODO are respectively the percent contribution of Diptera and Odonata to perch diet. Degrees of freedom associated with F-values in the univariate models (a) are 1,6 for age I+ fish, and 1,8 for age II+ and III+ fish. Degrees of freedom associated with F-values in the multivariate models (b) are 2,5 for age I+ fish, and 2,7 for age II+ and III+ fish.

Age classes	Model	F	p	r^2
(a)				
I+	RGR = −0.016 TN + 0.016	7.87	0.03	0.57
II+	RGR = −0.012 TN + 0.009	5.83	0.04	0.42
	ln RGR = −7.60 CN − 4.82	16.04	0.004	0.67
III+	ln RGR = −1.57 TN − 5.21	6.28	0.04	0.44
	ln RGR = −3.31 CN − 5.49	6.83	0.03	0.46
(b)				
I+	ln RGR = −1.23 TN + 34.49 RDR − 4.44	16.31	0.006	0.87
II+	ln RGR = −9.38 CN + 126.80 RDR − 5.70	128.32	0.0001	0.97
	RGR = −0.03 CN − 0.00005 DIP + 0.009	13.12	0.004	0.79
III+	RGR = −0.006 TN + 0.00003 DIP + 0.005	7.44	0.02	0.68
	ln RGR = −0.016 CN − 3.57 ODO − 5.38	9.27	0.01	0.73

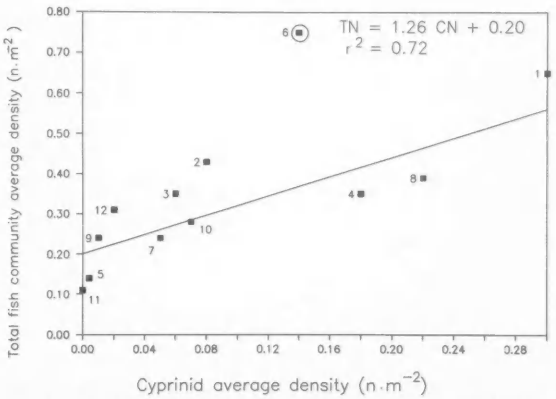

FIG. 4. Relationship between fish community average density (TN) and cyprinid average density (CN). The populations are identified using the legend in Fig. 1. Regression analysis was performed excluding Lake Hertel (6).

(age I+: $F_{1,6}=8.10$; $p<0.03$; $r^2=0.57$; age II+: $F_{1,8}=6.50$; $p<0.04$; $r^2=0.45$; age III+: $F_{1,8}=0.30$; $p>0.50$) and the average density of golden shiner (age I+: $F_{1,6}=1.73$; $p>0.20$; age II+: $F_{1,8}=33.96$; $p<0.0004$; $r^2=0.81$; age III+: $F_{1,8}=6.20$; $p<0.04$; $r^2=0.44$). While growth efficiency of both age I+ and II+ fish increased linearly with perch average biomass, it decreased with golden shiner average density.

The addition of the quantity of food consumed (Boisclair and Leggett 1989a) as a variable in models relating growth efficiency to fish species yielded only one significant relationship, this being for age I+ perch; the average density of pumpkinseed sunfish ($r^2=0.34$) and the quantity of food consumed by perch ($r^2=0.45$) explained a total of 79% of among-population variability in growth efficiency of age I+ perch ($F_{2,5}=9.51$; $p<0.02$). The growth efficiency of this age class was inversely related to the average density of pumpkinseeds and positively related to the quantity of food consumed by perch. We found no relationship between growth efficiency, fish average density, and food level for age II+ ($F_{2,7}=0.27$; $p>0.75$) and III+ perch ($F_{2,7}=1.19$; $p>0.35$). There was no significant relationship between the quantity of food consumed by age I+ perch and sunfish average density ($F_{1,6}=0.68$; $p>0.40$; $r^2=0.10$).

The combination of fish species and diet descriptors did not explain a significant fraction of among-population variability in perch growth efficiency ($p>0.05$).

Relationship between Growth Efficiency and Fish Community Functional Groups

For the models tested, only the average density of the total fish community and cyprinid average density explained a significant proportion of the among-population variability in growth efficiency (Table 8). The average density of the total fish community explained 43% of the among-population variability in the growth efficiency of age II+ perch. The average density of cyprinids explained 97% of the among-population variability in growth efficiency for age II+ fish and 36% of growth efficiency for age III+ fish. Growth efficiency consistently decreased as the densities of the total fish community and/or of cyprinids increased (Table 8). We found no significant relationship between the growth efficiency of age I+ perch and any fish community functional group ($p>0.05$). Moreover, the combination of fish functional groups and perch feeding levels in our analyses did not explain a significant fraction of among-population variability in growth efficiency ($p>0.05$).

Growth efficiency of age II+ perch decreased with increases in both the average density of the total fish community and the percent contribution of Ephemeroptera to the perch diet (Table 8). There was no significant relationship between the percent contribution of Ephemeroptera to perch diet and the average density of the total fish community ($F_{1,8}=0.50$; $p>0.50$; $r^2=0.06$). Growth efficiency of age III+ perch decreased with the average density of the total fish community, but increased as the percent contribution of Diptera increased in perch diet (Table 8). There was no significant relationship between the percent contribution of Diptera to perch diet and the average

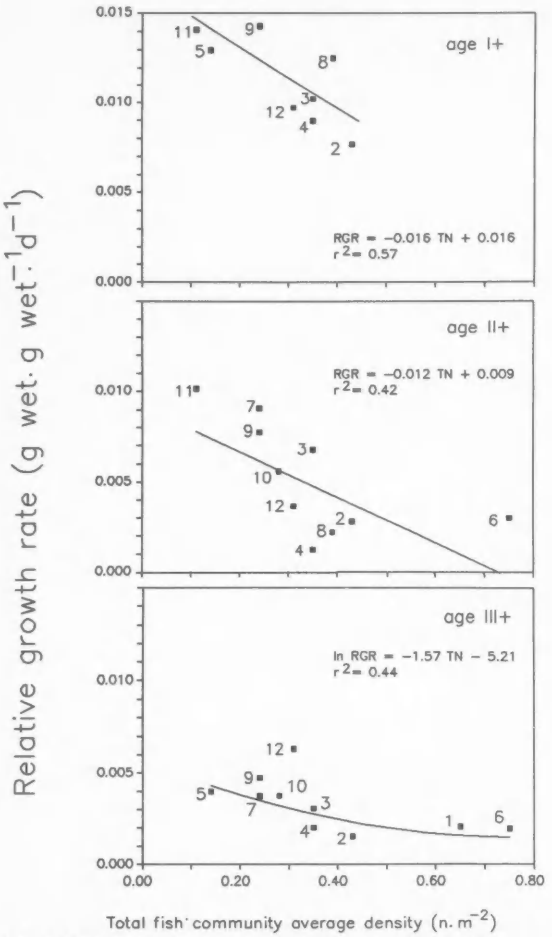

FIG. 5. Relationships between perch growth rates (RGR) and fish average density (TN). The populations are identified using the legend in Fig. 1.

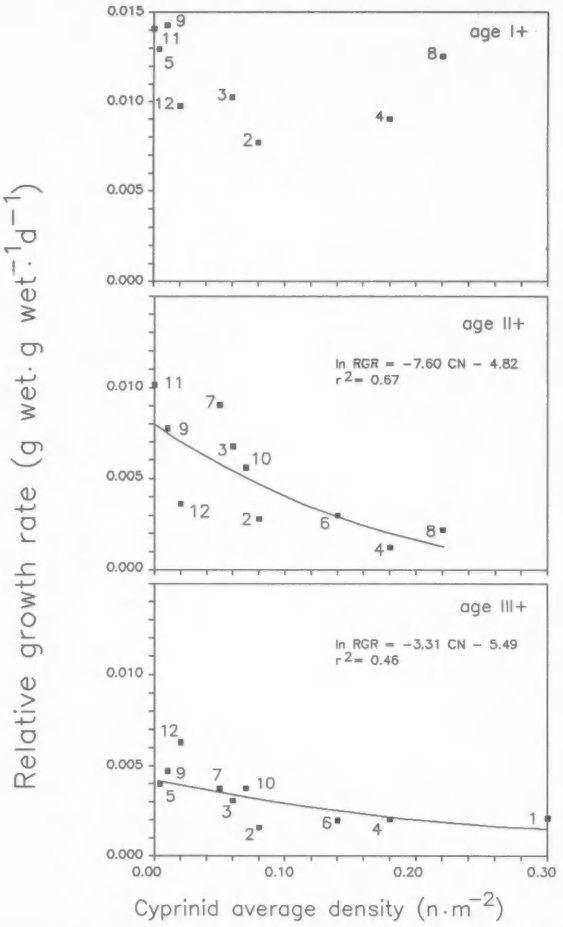

FIG. 6. Relationships between perch growth rates (RGR) and cyprinid average density (CN). The populations are identified using the legend in Fig. 1.

density of the total fish community ($F_{1,8}=0.83$; $p>0.35$; $r^2=0.09$).

Relationship between Fish Community Descriptors, the Quantity of Food Consumed, and Prey Type

The purpose of this paper is not only to test for the significance of relationships between perch growth and fish community descriptors but also to identify the means by which these descriptors influence fish growth. Our analyses demonstrate that there was no significant relationship between the fish community descriptors and other variables included in a given multivariate model. It is possible, however, that the relationship between perch growth rate and a particular fish community descriptor results from its covariation with some key element of perch diet not included in the model. In a previous paper we found that the percent contribution of Amphipoda, Diptera, and zooplankton to perch diets explained between 50 and 95% of among-population variability in perch growth rates or growth efficiency (Boisclair and Leggett 1989b). We thus tested for the significance of the relationship between the most important fish community descriptors (average density of fall fish, golden shiner, perch, sunfish; total fish community and cyprinid average density), and the forementioned key elements of perch diet.

We found no significant relationship between the percent contribution of Amphipoda, Diptera, and zooplankton to fish diet and any of the fish community descriptors that were themselves significantly related to perch growth rates or growth efficiency ($p>0.10$). These results, combined with the lack of significant relationship between the quantity of food consumed by perch and fish community descriptors, suggest that fish average density influences perch growth by means other than exploitative competition.

Discussion

In this study, we found the among-population variability in growth rates and growth efficiencies of age I+, II+, and III+ perch from 12 populations to be most strongly and consistently explained by the average density of the total fish community and/or the average density of cyprinids in the littoral zone of

TABLE 7. Statistics of the relationships between perch consumption rates (Boisclair and Leggett 1989a) and (a) fish community average density and (b) cyprinids average density. Degrees of freedom associated with F-values are 1,6 for age I+ fish, and 1,8 for age II+ and III+ fish.

	F	p	r^2
(a) Fish community average density			
I+	0.27	>0.60	0.04
II+	0.09	>0.75	0.01
III+	0.97	>0.35	0.11
(b) Cyprinids average density			
I+	0.43	>0.50	0.07
II+	0.95	>0.35	0.11
III+	1.64	>0.20	0.17

those lakes they inhabited. Multivariate analyses of several fish community descriptors, perch daily ration (Boisclair and Leggett 1989a), and several perch diet descriptors (Boisclair and Leggett 1989b) revealed that among-population variability in perch growth was best explained by the average density of the associated fish community and the quantity of food consumed. Perch growth rates were generally negatively related to fish average density and positively related to their feeding levels. Fish average density typically explained approximately 60% of the among-population variability in perch growth rates. Approximately 30% of the observed variance in growth rates was explained by the quantity of food consumed.

Exploitative competition is believed to take place when a negative relationship between fish growth and density occurs, together with a negative relationship between either the quantity or the quality of food consumed and fish density (see introduction). While the results of our analyses generally support the frequently reported negative relationship between fish growth and density (Brocksen et al. 1970; Backiel and LeCren 1978; Hansson 1985; Osenberg et al. 1988), the lack of significant relationship between the quantity or the type of food consumed by perch and many fish community descriptors does not substantiate exploitative competition as a principal mechanism. We believe, that the different perspectives provided by our multi-population comparative approach and the more controlled experimental approach are partly responsible for the contrast between our results and many previously published works on the mechanisms by which fish density influence growth.

Relationship between Fish Density and the Quantity of Food Consumed

The frequently observed negative relationship between fish growth and fish density has repeatedly been interpreted as evidence of a negative relationship between the quantity of food consumed by individual fish and fish density (for example see Craigg-Hine and Jones 1969; Powers 1974; Mortensen 1977; Penczak et al. 1981; Peterman 1894; Zalewski et al. 1985). The methodological difficulties associated with accurately assessing fish density and their food consumption rates in situ has, no doubt, contributed to the paucity of field tests of this assumed relationship.

To our knowledge, only one other field study has examined the relationship between estimates of the quantity of food consumed by fish, and fish community descriptors. Persson (1986) examined the influence of a selective reduction in the number of roach (*Rutilus rutilus*) in Lake Sovdeborg on the growth and food consumption of perch (*Perca fluviatilis*). A 40% reduction in roach biomass (70% reduction of the roach numerical abundance) was followed by a 140% increase in perch biomass (mainly young of the year fish). The quantity of food consumed by 0+ to 3+ perch increased two-fold following the reduction in the size of the roach population (Persson 1986).

Perssons (1986) approach to assessing the factors that structure fish communities was to examine the response to disturbance. We, in contrast, chose the comparative approach. Despite these differences, our general findings were similar; growth decreased as fish densities increased and increased as the quantity of food consumed increased. Our interpretations differ, however, regarding the association between fish densities and the quantity of food consumed. We found no evidence of a negative (or positive) relationship between the average density of the total fish community, or any subset of that community, and the quantity of food consumed. Perssons (1986) experiments, which demonstrated a relationship between fish density (roach) and fish growth (perch), operating via the quantity of food consumed, did so following what might be considered an extreme manipulation of the system (70% reduction in the roach numerical abundance).

Relationship between Fish Community Average Density and the Quality of Food Consumed

Many authors have inferred that fish community density acts on fish growth by diminishing the quality of food consumed. This inference is based on negative relationships between fish density and growth (Alm 1946, 1952; Deelder 1951; LeCren 1958; Henderson and Brown 1985; Henderson 1985). This interpretation has been supported by many detailed experimental studies of fish growth, density, and diet (Werner and Hall 1977; Hanson and Leggett 1986; Persson 1986, 1987; Mittelbach 1988).

We observed a significant negative relationship between perch growth and fish average density in each of the three age classes studied. However, we did not find any significant relationship between the average density of the total fish community and the present contribution of prey taxonomic groups to perch diet (Boisclair and Leggett 1989b). Our results are consistent with the results of Hansson (1985) on perch growth at 10 sites on the Baltic archipelago. Using the comparative approach, he observed a significant negative relationship between perch growth and density. There was, however, no evidence of a relationship between perch diet and perch density.

Whether the comparative or the experimental approach provides the most informative perspective on the relationship between fish density and growth is debatable. We recognize that the comparative approach we used is limited by the capacity of our sampling gear and schedule to provide a precise description of the littoral zone fish community relative to the questions addressed by our study. As such, our average density or biomass estimates represent broad indices of potential interactions among fish and not the actual level of interaction. It is our contention, however, that our results, though not as precise as those of experimental studies, more accurately represent field situations.

'Specific' Nature of the Relationship Between Fish Growth and Fish Density

Our analyses suggest that differences in whole fish community average density are more important to perch growth

TABLE 8. Significant relationships ($p<0.05$) observed between (a) growth efficiency (K_1) and fish community functional groups (TN = total community average density; CN = cyprinid average density) and (b) growth efficiency, fish community functional groups, and diet descriptors (Boisclair and Leggett 1989b). DIP and EPE are respectively the percent contribution of Diptera and Ephemeroptera to perch diet. Degrees of freedom associated with F-values in the univariate models (a) are 1,6 for age I+ fish, and 1,8 for age II+ and III+ fish. Degrees of freedom associated with F-values in the multivariate models (b) are 2,5 for age I+ fish, and 2,7 for age II+ and III+ fish.

Age classes	Model	F	p	r^2
(a)				
I+	None	5.92	0.04	0.43
II+	$K_1 = -19.79\ TN + 16.72$	222.51	0.0001	0.97
	$\ln K_1 = -9.17\ CN + 2.88$	6.17	0.04	0.44
III+	$\ln K_1 = -4.95\ CN + 2.21$			
(b)				
I+	None			
II+	$\ln K_1 = -3.04\ TN - 0.03\ EPE + 3.52$	9.78	0.009	0.74
III+	$\ln K_1 = -2.85\ TN + 0.01\ DIP + 2.49$	8.51	0.01	0.71

rates than attributes of any single fish species. This interpretation is not incompatible with experiments on the relationship between fish growth and density. These experiments have been concerned primarily with the analysis of exploitative competition on either an intra- or inter-specific basis, and have generally focussed on the interactions between one or two species (Schmith and Coyer 1983; Tonn 1985; Rose 1986; Kennedy and Strange 1986; Hearn 1987; Gunn et al. 1987; Tonn and Paszkowski 1987; but see Werner and Hall 1979 for a three species study). The majority of the inter- or intraspecific competition experiments that have shown strong effects of fish density on growth have involved analyses of species that accounted for a large portion of the total fish community in the systems studied. In Persson's (1986) study of roach and perch, these two species accounted for 98% of the total fish community. Werner et al. (1983), and Werner and Hall's (1977, 1979) competition experiments were conducted in experimental ponds containing only the two or three species manipulated. Hanson and Leggett's (1985, 1986) experimental study of the intra- and interspecific competition between the yellow perch and the pumpkinseed sunfish involved species that comprised between 60% (Hanson and Leggett 1985) to 83% (this study) of the total littoral zone fish average biomass. These competition experiments were performed in enclosures containing only two species at densities corresponding to whole fish community density. Mittelbach's (1988) study of pumpkinseed and bluegill sunfish (*Lepomis macrochirus*) was similarly conducted in habitats in which these species represent 60 to 70% of the total fish community (Werner et al. 1977). Other examples in which only two fish species were monitored are found in Schoener (1983) and Hearn (1987). In many experiments, the manipulation of the densities of one to two fish species can therefore be considered equivalent to whole fish community treatment.

The results of our studies are consistent with the repeated demonstration of the potential negative effects of fish interactions on growth. We observed, for example, negative effects of the average densities of perch, sunfish, and golden shiner on perch growth. As for intra- and inter-specific competition experiments cited above, those species found to have a significant influence on perch growth were the most abundant in the systems studied. We also found that there were strong correlations among the average densities of the community descriptors that explained perch growth. For instance, the correlation between pumpkinseed average density and total fish community average density was 0.69, and that between golden shiner and cyprinid average density was 0.85. It is important to note, however, that a greater contribution to explained variance in perch growth was achieved by the analysis which included larger functional groups (i.e. total community and cyprinids). Consequently, the specific composition of the fish communities studied appears to have a smaller influence on perch growth than do attributes of larger functional groups.

Our intent in making this point is not to diminish the importance of species/species interactions. Rather we emphasize that the effect of average density of the fish community as a whole may operate on growth in ways which have not yet been fully explored.

An Alternate Hypothesis to Explain the Relationship between Fish Growth and Fish Average Density

Our study indicates that the average density, and not the biomass, of fish community descriptors explains the variance in perch growth rates. We also found the average density of the total fish community, and not attributes of single species, best accounts for perch growth differences. Furthermore, exploitative competition does not appear to be the mechanism by which fish average density influences fish growth.

The only hypothesis we find compatible with these results is that the strong and consistent negative relationship between perch growth and the fish average density results primarily from among-population differences in activity levels induced by among-lake variability in fish average density and community interactions (i.e. nonexploitative interactions). The most important prediction of this hypothesis is that fish activity rates should increase as fish average density increases. While this prediction remains to be tested directly, circumstantial support is provided by many experiments.

Numerous experiments have demonstrated that the presence of a predator directly influences fish distribution, habitat use, diet, foraging efficiency, and ultimately fish growth (Werner et al. 1983; Mittelbach 1983, 1988; Milinski 1986). Predator presence is generally believed to operate either by restricting fish to less profitable habitats (Werner et al. 1983; Mittelbach 1983;

Milinski 1986) or by decreasing the time available for foraging through increases in foraging latency (Milinski and Heller 1978; Street et al. 1984; Lendrem 1984; Morgan and Colgan 1987). Numerous experiments have also shown that the presence of conspecifics increases feeding rates through social facilitation (Shaw 1969; Lazarus 1979; Olla and Samet 1974; Pitcher and Magurran 1983; Giraldeau 1984; Morgan and Colgan 1987) or by decreasing individual vigilance to predators (Morgan and Godin 1985; Pitcher 1986). Still other experiments have determined that the presence of conspecifics can decrease fish feeding rates through agonistic interactions (Fenderson et al. 1968; Fenderson and Carpenter 1981; Hodapp and Frey 1982; Street et al. 1984; Paszkowski 1985). The existence of a density-dependent energy expenditure is supported by Caraco et al. (1980) who showed that social interactions, which are more frequent at high densities, can decrease foraging success, and eventually growth, by means other than direct exploitative competition. Iles (1973) reached similar conclusions and attributed the effect to 'crowding'.

Each experiment emphasizes one type of intra- or inter-specific interaction. However, it can be expected that wild fish facing a multispecies environment having patchy food distributions, would display a composite of these behaviors. The fact that the average density of the total fish community was the best and most consistent contributor to the explained variance in among-population growth suggests that this variable may represent an integrated measure of the activity costs (and benefits) associated with community interactions.

Taken together, our data suggest that while both exploitative competition and nonexploitative interactions may contribute to the among-population differences in perch growth rates we assessed, nonexploitative interactions are dominant.

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Influence of Cover Complexity and Current Velocity on Winter Habitat Use by Juvenile Coho Salmon (*Oncorhynchus kisutch*)[1]

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McMahon, T. E., and G. F. Hartman. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 46: 1551–1557.

Winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) varied with cover type and flow level in outdoor stream channels. Cover utilization and the number of fish remaining in stream channels increased significantly as cover complexity increased. Most fish emigrated during a simulated freshet unless the most complex cover (low velocity, shade, and wood debris combined) was available. At both high and low flows, emigration occurred primarily during the rapid decline in light levels at twilight. Most coho formed aggregations beneath cover, exhibiting feeding and aggression at temperatures as low as 2.5°C. We conclude that (1) social interactions, in concert with habitat features, influence the abundance of coho salmon within specific stream habitats in winter, and (2) structural complexity of wood debris is an important consideration for management practices designed to protect or enhance winter habitat for this species.

L'habitat utilisé en hiver par les saumons cohos juvéniles (*Oncorhynchus kisutch*) variait en fonction du type de couvert et du débit dans les chenaux extérieurs. L'utilisation du couvert et le nombre de poissons restant dans les cheneaux augmentait nettement en fonction de la complexité du couvert. La plupart des poissons émigraient pendant une crue simulée à moins de disposer du couvert le plus complexe (faible vitesse, ombre et débris de bois combinés). Que le débit soit fort ou faible, l'émigration se produisait surtout pendant la rapide baisse de l'éclairement au crépuscule. La plupart des cohos se tenaient en groupe sous le couvert, présentant des comportements d'alimentation et d'agression à des températures pouvant descendre jusqu'à 2,5°C. Nous en concluons que 1) les interactions sociales, combinées aux caractéristiques de l'habitat, influent sur l'abondance du saumon coho dans certains habitats lotiques précis en hiver et que 2) la complexité structurale des débris de bois est un aspect important à considérer dans les pratiques de gestion visant à protéger ou à améliorer l'habitat hivernal de cette espèce.

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Over the past decade, the behavior and ecology of stream-dwelling salmonids during winter has received considerable attention. High mortality rates and different, often more restrictive, habitat requirements during winter (e.g. Mason 1976; Rimmer et al. 1984; Cunjak and Power 1986) have emphasized the importance of this season to salmonid management. Because the quality and quantity of cover appears to be a major factor governing overwinter survival (e.g. Hunt 1969; Mason 1976; Tschaplinski and Hartman 1983), research has focused on defining winter cover requirements.

For juvenile coho salmon (*Oncorhynchus kisutch*), large wood debris provides a major component of winter cover (Hartman 1965; Bustard and Narver 1975a; Tschaplinski and Hartman 1983; Heifetz et al. 1986). Wood debris is thought to provide protection from predators during this period of low water temperatures, and from downstream displacement from high velocities by frequent and at times severe winter freshets that characterize coastal systems (Hartman 1965; Bustard and Narver 1975a). Recent studies have documented that (1) higher numbers of coho salmon remain within accumulations of wood debris after winter freshets than in other types of stream habitats (Tschaplinski and Hartman 1983), (2) the number of overwintering coho salmon is positively correlated with the volume of debris (Tschaplinski and Hartman 1983; Martin et al. 1986), and (3) the number of overwintering coho is low in stream reaches where debris abundance has been reduced by debris removal associated with streamside logging (Tschaplinski and Hartman 1983; Murphy et al. 1986) or other disturbance (Martin et al. 1986).

Although previous studies have established the importance of debris in providing winter cover for coho salmon, the characteristics that determine its suitability have not been clearly defined. The objective of this study was to examine selection of various cover types by coho salmon. The effects of high current velocities on cover selection were also examined, because population declines during winter have often occurred in conjunction with freshets (Mason 1976; Tschaplinski and Hartman 1983).

Materials and Methods

Test Channels and Fish

Experiments were conducted in outdoor stream channels that allowed fish either to become residents or emigrate in response

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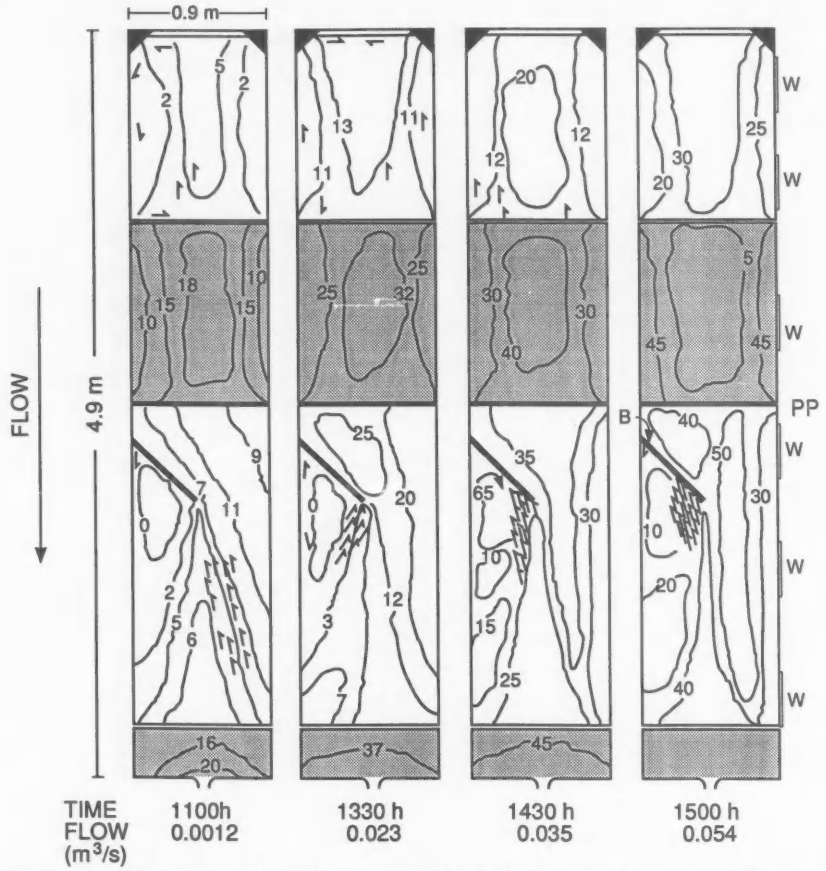

FIG. 1. Stream channel dimensions and representative distribution (arrows) of coho salmon in relation to velocity isopleths (cm/s) before (1100 h) and during (1330, 1430, 1500 h) a simulated freshet in stream channels having a baffle cover structure. PP = plunge pool at pool–riffle interface, W = windows. Shaded sections = riffles, unshaded = pools.

to manipulations of cover features and current velocity. The pair of channels (each $4.9 \times 0.9 \times 0.6$ m) (Fig. 1) was constructed adjacent to Dicks Creek, a tributary of Carnation Creek, a small stream located on the west coast of Vancouver Island (see map, Bustard and Narver 1975a). Channels contained a gravel (2–6 cm in diameter) substrate and two alternating sequences of pools (depth 23.5 cm) and riffles (depth 6.4 cm). A flume carried water from Dicks Creek to a common header box, and water flow into each channel was controlled by boards in the header box and the flume. A dam located at the outlet of Dicks Lake, 1 km upstream from the channels, allowed us to release large quantities of water into the channels to simulate a freshet. A 0.6-cm-mesh screen was placed at the upstream end of the channels to prevent fish from entering the header box. Emigrating fish were captured in a net positioned at the downstream end.

Wild coho used in experiments were captured during December 1985 from the Sarita River (2 km south of Carnation Creek) with baited minnow traps. Fish were held in outdoor tanks supplied with a constant flow of Dicks Creek water and fed frozen euphausids daily. One hour prior to tests, coho were mildly anesthetized in a 2-phenoxyethanol solution and their fork length was measured to the nearest millimetre. At least 1 wk elapsed prior to re-use of fish in experiments.

Cover × Flow Experiments

Four types of cover and two levels of flow were used to test winter cover use. In order of increasing complexity, cover types were:

(A) No cover: channel lacked any in-stream or overhead cover.

(B) Baffle: low velocity refuge as provided by a submerged log was simulated by a 25 × 45 cm plywood sheet attached at a 45° angle to the side of the channel in the upstream half of the second pool.

(C) Baffle/shade: an undercut bank providing both overhead shade and low velocity refuge was simulated by extending a 36×91 cm plywood sheet extending downstream from the top of the baffle, and positioned 5 cm above the water surface.

(D) Baffle/shade/simulated root mass: a debris jam providing low velocity refuge, shade, and a com-

plex of interstitial spaces was simulated by placing a 25 × 36 × 91 cm 'root mass' (six alternating layers of 3–6 cm diameter limbs) beneath the baffle/shade structure.

The two flow levels used in experiments were "low flow" and "high flow," the latter simulating the rising flow pattern of a freshet. During low flow, mean bottom velocity was 15 cm/s in riffles and 3.5 cm/s in pools when no cover (cover type A) was present. During a simulated freshet, mean bottom velocity was 60 cm/s in riffles and 28 cm/s in pools at maximum flow (Fig. 1). Velocity was measured 5 cm above the substrate at three points along six equidistant transects across each channel with a Gurley pygmy current meter. Low and high flows corresponded to average bottom velocities determined from measurements made along pool and riffle transects of Carnation Creek when discharge at the main hydrological weir was at base winter low (0.23 m^3/s) and during a small-magnitude freshet (2.26 m^3/s), respectively. Winter flows in Carnation Creek fluctuate widely and rapidly from about 0.2 m^3/s up to 64.9 m^3/s; annual peak winter flows averaged 35 m^3/s from 1971 to 1986 (Tschaplinski and Hartman 1983; Hetherington 1988).

During each 46-h trial, the type of cover in the experimental channels was the same. At 1100 h on day 1 of an experiment, 20 coho ranging in fork length from 54–77 mm ($\bar{x} = 64.6$ mm) were added to each channel. For the first 24 h, rear exits were blocked and low flows were maintained in both channels to allow fish to acclimate. At 1100 h on day 2, rear exit screens were removed, and fish had the choice of remaining in or leaving channels over the next 22 h. In one channel, low flow was maintained for the remainder of the trial. In the other, fish were exposed to a simulated freshet (high flow) by increasing the release of water from the header box every 30 min from 1300 to 1500 h (Fig. 1). Maximum discharge was then maintained for the remainder of the trial (18 h). At 0900 h on day 3, channels were drained and remaining fish counted and measured.

Two trials of this procedure were performed for each of the four different combinations of cover. The relatively short test period (46-h) was considered representative of the patterns of residency, emigration, and habitat use exhibited by coho over longer periods since fish readily acclimated to experimental conditions (see below). In a more direct test of this assumption, Taylor (1988) found that, over a 1-mo observation period, microhabitat use by coho in laboratory stream channels remained stable after as little as 24 h. The low variation in patterns of cover use and emigration in our experiments lent additional support to our assumption.

Trials were run from 15 December 1985 to 5 March 1986. Fish were not artificially fed during experiments. Natural insect drift entered channels from Dicks Creek. Drift net samples taken from the flume indicated the amount of drift available during an experiment was low. Water temperatures ranged from 2.0 to 8.3°C, but were usually 5–6°C; temperature extremes never exceeded 1.8°C during an experiment. During the winter high flow period in Carnation Creek (October–March), average daily temperatures ranged from 2–9°C and were usually 4–6°C (Bustard and Narver 1975a; Brown and McMahon 1988). Bustard and Narver (1975a) found that cover-seeking behavior of juvenile coho salmon during this period was most pronounced at temperatures <7°C. Moderate increases in turbidity occurred in stream channels during high discharge (actual levels not measured), but declined to a level where an observer could easily see across the channel within 1 h after maximum flow was attained (1600 h).

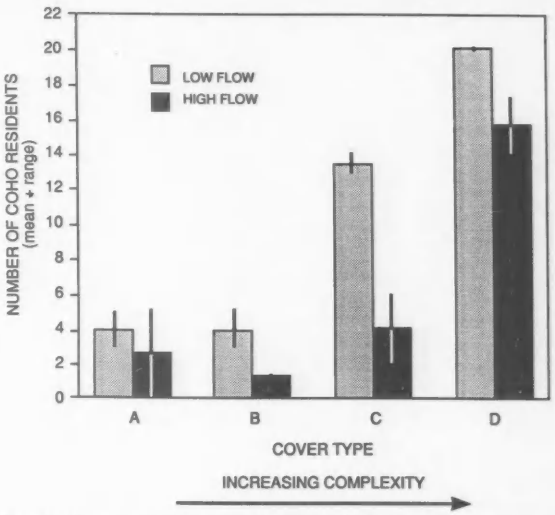

FIG. 2. Mean number (± range) of juvenile coho salmon remaining in stream channels with cover × flow combinations (A) no cover; (B) baffle; (C) baffle/shade; and (D) baffle/shade/root mass.

Fish were observed through slits in black plastic curtains covering six windows located along one side of each channel. Fish appeared to readily acclimate to experimental channels. Fright responses (rapid swimming, rapid breathing, tight grouping, and bleached coloration) subsided within 1 h and normal feeding and aggressive behaviors occurred within 6 h of release. After this 6-h period, observations of cover use, feeding, and aggression were made at least once each morning and afternoon along the length of each channel.

Cover use was defined as the percent of fish in the channel occurring within 15 cm behind or under a cover structure. Cover use was based on observations of ≥15 fish; fish numbers varied due to emigration. Use of cover at high flow was determined during the 2-h period of flow increase. Use of cover by coho inhabiting the darkened shade or simulated root mass cover structures was determined by subtracting the number of fish away from cover from the total number of fish present.

Rates of feeding were determined by counting the number of feeding acts and rates of aggression by counting the number of aggressive acts (nipping, chasing, lateral display, sensu Hartman 1965) observed in groups of 3–15 fish for 10 min during low-flow conditions. Feeding rates of coho in groups of less than three fish were not counted since feeding tended to be sporadic and variable among individuals and hence did not accurately reflect trends in feeding of the entire group of coho inhabiting a channel. Observations of feeding and aggression of fish occupying the shade or simulated root mass cover structures were made on fish occurring along the edge of cover.

Fish behavior was monitored during simulated freshets and their distribution was recorded at least every 30 min during daylight hours. Emigrants were removed from nets and measured at least hourly from 1200–2000 h (every 15 min during periods of high emigration) and again at 0900 h the next morning. Timing of emigration in relation to time of sunset, sunrise, and twilight was calculated from the Nautical Almanac (Anonymous 1986) corrected for the latitude and longitude of Carnation Creek (48°55′N, 125°00′W).

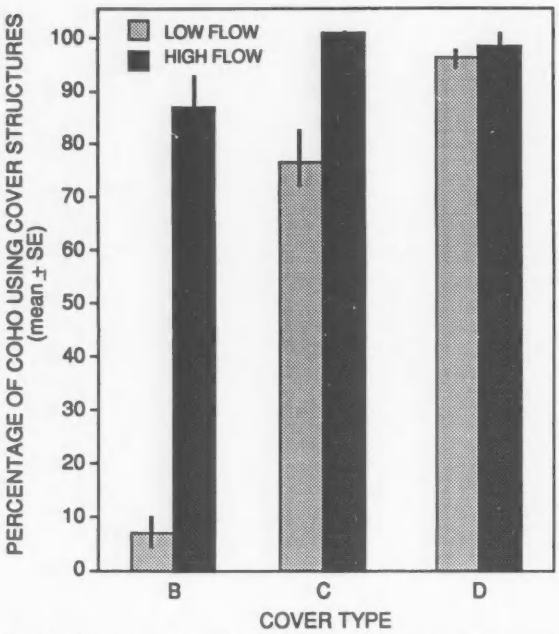

FIG. 3. Mean percentages (±SE) of coho salmon using cover types (B) baffle; (C) baffle/shade; and (D) baffle/shade/simulated root mass at low and high flows.

Results

The number of coho remaining in stream channels (Fig. 2) varied significantly among cover types (Friedman's two-way ANOVA, Zar 1984; $\chi_r^2 = 11.37$, $p < 0.01$) and flow levels ($\chi_r^2 = 7.0$, $p < 0.01$). During low flow trials, less than five coho remained in channels when no cover or a baffle was present. The number of residents increased markedly with the addition of overhead shade. When the root mass was added, all 20 fish introduced at the start of the experiment remained in the channels. Further, few coho remained in channels during a freshet unless the baffle/shade/root mass structure was present. Pairwise comparisons of each cover × flow treatment demonstrated that, at both high and low flows, significantly more coho remained in channels during trials with the root mass than when other cover types were available (Fig. 2; Duncan's multiple range tests on ranked data, $p < 0.05$).

Coho behavior and distribution also varied with cover type and flow. At low flow, during trials with either no cover or a baffle present, coho occurred in front or rear pools in aggregations of >15 individuals, where water velocity was 2–7 cm/s; no fish were observed in riffles and only a few were observed in the lee of the baffle where velocity was near zero (Figs. 1 and 3). When overhead shade was added, coho use of the cover structure increased significantly (arcsine transformation of percentages, $t = 9.21$, $df = 18$, $p < 0.001$). Cover use increased significantly again when the baffle, shade, and simulated root mass were combined ($t = 2.47$, $df = 18$, $p < 0.05$) (Fig. 3). At low flow, therefore, increased use of cover was accompanied by an increase in the number of fish remaining in channels. Cover use was similar when channels were closed (during acclimation) or open to emigration (t-tests, $p > 0.3$).

As water velocity was increased during a simulated freshet, use of cover also increased (Figs. 1 and 3). During no cover trials, coho oriented downstream in the plunge pool at maximum flow, but had difficulty maintaining position in the turbulence, and most fish later emigrated from the channel. During trials with a baffle or a baffle/shade structure, fish formed a tight group that swam against the eddy behind the baffle (Fig. 1). Bottom velocity at this location averaged 10 cm/s at maximum flow; however, high turbulence made it difficult for coho to maintain position. In contrast, the addition of a simulated root mass to the baffle/shade structure provided an effective refuge from high velocity and turbulence. At maximum flow, water velocity in the downstream half of the cover structure was 14 cm/s, but velocity and turbulence directly behind the baffle was near zero.

Emigration occurred predominantly during twilight (Fig. 4). Seventy-five percent of the total number of coho emigrating from channels during a freshet and 61% of the total emigrating from channels with low flow did so during the period of rapidly decreasing light intensity from 30 min before to 60 min after sunset; an additional 23% of coho emigrating from channels with low flow left early the next morning. This emigration pattern was consistent throughout the experimental period, despite a progression in the time of sunset of ~90 min.

Physical displacement of coho by high current velocities did not appear to be the primary cause of emigration during simulated freshets. During a freshet, coho maintained their position in the lee of a baffle or in the plunge pool, but as light levels decreased they swam higher in the water column and then were swept downstream. Only 17% of all emigrants from high flow channels (18 of 105) left channels during the ~4 h period of high flow before sunset (Fig. 4) and only four fish were found impinged on the rear screen that covered most of the downstream end of the channels. Few fish left channels during the ~2 h period of higher turbidity following the increase in flows (Fig. 4).

Feeding and aggression occurred during all trials and were observed at temperatures as low as 2.5°C. Neither rates of feeding (means = 1.4–4.7 acts per 10 min; Kruskal–Wallis one-way ANOVA, $H = 2.38$, $P = 0.49$) nor aggression (means = 0.6–1.2 acts per 10 min; $H = 1.79$, $P = 0.41$) differed significantly between trials with different cover types. Aggression was less pronounced and less frequent than that reported at higher temperatures (Hartman 1965; Glova 1986), occurring most frequently when one to two fish excluded all others from territories established during brief (<30 min) feeding bouts at the interface of fast and slow currents near the edge of cover. When the root mass was present, coho were evenly distributed within the structure ~15–20 cm apart and defended small areas around these sites primarily by erecting the dorsal fin whenever another fish swam close by, and occasionally by nipping or chasing intruders.

Size differences between residents and emigrants were not significant in most trials (Table 1). Residents tended to be smaller than emigrants in trials lacking the root mass and larger than emigrants when the root mass was present, but in only three trials were differences statistically significant. The four coho found impinged on the rear screen during a freshet were all in the smallest 5-mm size range used, suggesting that small coho were most susceptible to downstream displacement.

Discussion

Structurally complex accumulations of large wood are an important component of winter habitat for juvenile coho

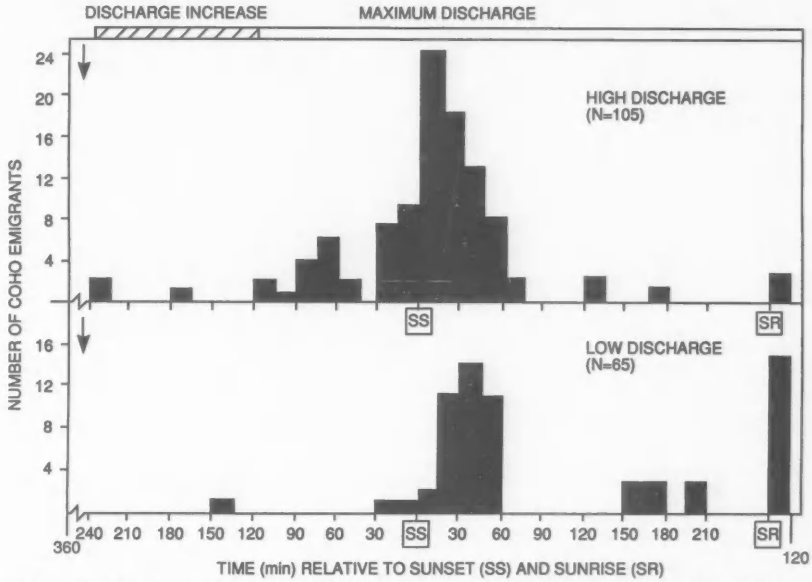

FIG. 4. Number of coho salmon emigrating from stream channels in relation to time of day during both high- and low-flow trials. Data combined for the eight trials at each flow level (N = total number of emigrants). Vertical arrow indicates when rear exit screens were removed.

TABLE 1. Mean lengths and differentes (t-test) between mean lengths of resident and emigrants coho salmon in cover × flow experiments (number of fish in parentheses). Initial refers to fish introduced into stream channels at the start of the experiment.

Cover[a] × flow[b] treatment	Mean fork length (mm)			
	Initial	Residents	Emigrants	t
A × LF	62.8	56.0 (3)	63.8 (17)	2.45[c]
	66.1	61.0 (5)	66.8 (15)	−1.57
A × HF	62.8	— (0)	62.8 (20)	—
	66.1	65.8 (5)	66.3 (15)	−0.15
B × LF	63.1	58.0 (3)	66.3 (17)	2.16[c]
	68.5	65.8 (5)	69.6 (15)	−1.14
B × HF	63.8	53.0 (1)	63.8 (19)	—
	66.0	64.0 (1)	66.0 (19)	—
C × LF	63.1	64.3 (13)	61.6 (7)	+0.43
	66.5	64.6 (14)	70.7 (6)	2.15[c]
C × HF	63.3	59.5 (2)	64.8 (18)	−1.09
	66.4	63.8 (6)	67.0 (14)	−1.07
D × LF	66.8	66.8 (20)	— (0)	—
	66.1	66.1 (20)	— (0)	—
D × HF	65.9	66.4 (14)	65.0 (6)	+0.33
	66.0	66.6 (17)	62.0 (3)	+1.15

[a]A = no cover, B = baffle, C = baffle/shade, D = baffle/shade/root mass.

[b]LF = low flow, HF = high flow.

[c]$p<0.05$.

salmon. The results of our experiments support previous field and experimental studies which demonstrated that during winter coho occupy pools and undercut banks containing large wood or root wads and are generally absent from main-channel habitats lacking such cover (Bustard and Narver 1975a,b; Tschaplinski and Hartman 1983; Heifetz et al. 1986; Brown and McMahon 1988). Our study demonstrated that coho abundance increased as cover complexity increased, with only the most complex structure supporting significant numbers of fish during simulated freshets. As in studies of cover selection in brown trout (*Salmo trutta*; Hartman 1963), we found that the most suitable winter cover for coho combined all three environmental features of low velocity, shade, and three-dimensional complexity.

Cover requirements of coho during winter differ from, and are generally more restrictive than those during summer. In summer, coho occupy a wide range of stream habitats, including pools, side channels, glides, and the edges of riffles (Bisson et al. 1982; McMahon 1983; Murphy et al. 1986). Current velocity is often considered the primary variable governing microhabitat selection by salmonids during summer (e.g. Shirvell and Dungey 1983; deGraaf and Bain 1986). We found that slow current velocities are important to coho in winter habitat selection, but only when in conjunction with cover that provides shade and three-dimensional complexity (see also Bustard and Narver 1975a). The preference by coho for shade during winter contrasts sharply with Ruggles' (1966) findings that the number of resident coho decreased by nearly 50% during summer when overhead shade was added to his experimental channels. Such a response may be related to a general increase in photonegative behavior among salmonids during winter (Bustard and Narver 1975a; Cunjak 1988).

Shifts into high cover, low velocity microhabitats during winter appear to be characteristic of many stream-dwelling salmonids (Chapman and Bjornn 1969; Bustard and Narver 1975a; Rimmer et al. 1984; Cunjak and Power 1986). Types of cover utilized as overwintering habitat vary depending on species, fish size, temperature, and hydrologic regime (Bustard 1986; Cunjak and Power 1986). In addition to their use of large woody

debris as winter habitat, coho also overwinter in lakes and in off-channel ponds, swamps, sidechannels, and tributaries (Peterson 1982a, 1982b; Swales et al. 1988; Hartman and Brown 1988). In these habitats, too, coho are found in close association with woody debris or other types of complex cover such as emergent vegetation.

We observed two behaviors in coho that would minimize displacement during winter freshets. First, there was a strong preference for structurally complex cover; second, as velocities increased, coho shifted to the lowest-velocity microhabitats available and then emigrated (chiefly during twilight) from areas that failed to provide shelter from high turbulence. Movements of coho from sites lacking wood into areas having suitable winter habitat have been described for a number of streams coincident with declining temperatures and increasing flows in autumn (e.g. Peterson 1982a, 1982b; Tschaplinski and Hartman 1983; Brown and McMahon 1988). Emigration from these areas during twilight may serve to decrease mortality from visual predators during shifts in habitat (Helfman 1981a).

In coastal streams, these behaviors are undoubtedly important for survival of young coho during winter when freshets are common and swimming abilities are reduced. Based on data from Glova and McInerney (1977), we calculated that at 3°C the critical swimming speed of coho 60-mm long is 22 cm/s, ~50% less than that at summer temperatures (18–23°C). Bottom velocity in open pools and riffles in Carnation Creek commonly exceeds this level even during relatively small freshets (e.g. 2.26 m^3/s). Both this study and that of Tschaplinski and Hartman (1983) indicate that debris serves to dissipate the energy of flowing water and create pockets of shelter from high current velocities. In a recent analysis of pool-forming features in various coastal streams in Oregon, Kaufmann (1987) found that the size of pools and the volume of low velocity zones present at high flows was positively related to the structural complexity of debris.

Use of structurally complex cover by coho salmon during winter is likely also to minimize predation risk (Werner et al. 1983). A. Dolloff's (U.S. Forest Service, Blacksburg, VA 24061, pers. comm.) recent count of 230 juvenile coho salmon and Dolly Varden charr (*Salvelinus malma*) otoliths in one river otter scat collected next to a beaver pond in southeast Alaska points to the potentially high predation rates on coho during winter. The preference of coho for shade as shown in our study may also minimize predation by providing camouflage and by enhancing detection of predators (Helfman 1981b).

Although aggression diminishes in winter and coho commonly form aggregations under cover (Hartman 1965; Mason 1965; Glova 1986, this study), we found that coho continue to exhibit agonistic behaviors. High structural complexity of wood debris may serve an additional function of reducing the frequency of agonistic interactions by increasing the visual isolation of individual fish (Dolloff 1986). This may explain the significant increase in numbers of coho of all sizes remaining in stream channels when the root mass was added to the baffle/shade cover structure.

The results of our experiments emphasize the importance of protecting and/or enhancing the structural complexity of wood debris for proper management of coho salmon habitat. The abundance and structural integrity of wood debris can be substantially reduced after streamside logging, stream cleaning, and other forest management practices (Bisson et al. 1987). In Carnation Creek, stream reaches impacted by logging had 93% less wood volume and a 75% fewer overwintering coho than nonimpacted reaches (Tschaplinski and Hartman 1983; Brown and McMahon 1988). Since accumulations of large wood remain low for at least 50 yr after debris loss (Grette 1985; Martin et al. 1986; Andrus et al. 1988), winter habitat for coho salmon in the mainchannels of debris-impoverished streams is likely to be reduced for many decades. Winter habitat for coho can best be maintained during and after logging by leaving wood debris in the stream and ensuring its continued recruitment by leaving buffer strips of trees along streambanks (Tschaplinksi and Hartman 1983; Heifetz et al. 1986). Protecting clumps of trees along certain stream sections could increase the possibility that natural processes of windthrow and bank undercutting introduce wood into the channel in multiple configurations (Sedell et al. 1984; Bisson et al. 1987).

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Comparison of Heavy Metals in Two Groups of Ringed Seals (*Phoca hispida*) from the Canadian Arctic

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Wagemann, R. 1989. Comparison of heavy metals in two groups of ringed seals (*Phoca hispida*) from the Canadian Arctic. Can. J. Fish. Aquat. Sci. 46: 1558–1563.

Heavy metals (Pb, Hg, Cd, Cu, and Zn) and Se and As were determined in liver, kidney, and muscle of ringed seals captured near a lead–zinc mine in the Strathcona Sound area, and in a reference group from Admiralty Inlet in the Canadian Arctic. The mean concentrations of Pb in liver and muscle and Se in muscle were higher in seals shot near the mine area than in a reference group shot 50–75 km from this area, notwithstanding large variances in metal concentrations arising from inter-metal and Hg–age and Cd–age positive correlations. Strong positive correlations were found between age of animals in the reference group and Cd in kidney and Hg in liver, between Se and Hg in liver, and a negative one between age and Cu in the three tissues examined. Nearly half of the individuals in the mine-area group were shown, by multiple linear regression, to have higher Hg, Pb, or Cd than the reference group. High Cd concentrations were found in tissues of seals from both groups.

On a mesuré les métaux lourds (Pb, Hg, Cd, Cu et Zn) ainsi que Se et As dans le foie, les reins et les muscles de phoques annelés capturés près d'une mine de plomb et de zinc dans la région de la baie Strathcona, et chez un groupe témoin provenant de l'inlet Admirality, dans l'Arctique canadien. La concentration moyenne de Pb dans le foie et les muscles et de Se dans les muscles était plus élevée chez les phoques abattus près de la mine que chez le groupe témoin abattu à 50 ou 75 km de cette zone, en dépit des fortes variances dans les concentrations de métaux causées par les corrélations positives entre les métaux et entre l'âge et Hg et Cd. On a observé de fortes corrélations positives entre l'âge des animaux du groupe témoin et le Cd dans le rein et le Hg dans le foie, entre le Se et le Hg dans le foie, et une corrélation négative entre l'âge et le Cu dans les trois tissus examinés. Chez près de la moitié des individus du groupe de la mine, on a montré, par régression linéaire multiple, que la concentration de Hg, de Pb ou de Cd était supérieure à celle relevée chez le groupe témoin. On a observé de fortes concentrations de Cd dans les tissus des phoques des deux groupes.

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Native Arctic residents historically relied on fishes and marine mammals as sources of protein and fat in their diet. Although diet varies from community to community, some seal meat is consumed by most coastal Arctic people (Schaefer and Steckle 1980). A recent survey of the diet of the native population of Broughton Island (D. Kinloch, Health and Welfare Canada, Yellowknife, NWT, pers. comm.) showed that ringed seal meat comprised 26% of their diet, and 43% of all meats consumed (seals, whales, fish, caribou, polar bear).

Previous studies (Wagemann et al. 1983; Smith and Armstrong 1975; Goldblatt and Anthony 1983) have shown that concentrations of heavy metals can be relatively high in tissues of some marine mammals from the Canadian Arctic and Alaska, particularly Cd in the kidney and liver and Hg in the liver. Ringed seal liver is a preferred food item to some natives. This could be a significant source of heavy metals to consumers.

Contamination of invertebrates and sediments with heavy metals and As in Strathcona Sound, near the marine terminal of the Nanisivik lead–zinc mine has been reported by Fallis (1982, p. 1), "Trace metals associated with the operation of the Nanisivik Mine . . .may gain entry into Strathcona Sound by a number of means, the most likely of which are tailings pond discharges into Twin Lakes Creek and accidental spills of lead and zinc concentrates during the loading of concentrate-carrying ships. Concentrates spilled on land may subsequently be transported to Strathcona Sound via wind action, precipitation, or meltwater run-off." Twin Lakes Creek discharges into Strathcona Sound. Others have also reported on metal concentrations in biota of various trophic levels in Strathcona Sound (Bohn and McElroy 1976; Bohn and Fallis 1978).

The ringed seal (*Phoca hispida*) is the most abundant marine mammal in the Canadian Arctic where it is a permanent resident. It is a general and opportunistic feeder (invertebrates and fishes), supports the polar bear population (*Ursus maritimus*) serving as its main dietary staple, and is of dietary and economic importance to coastal Arctic residents. The biology, distribution and behaviour of ringed seals has been amply described (McLaren 1958; Smith 1976, 1987; Ronald and Mansfield 1975).

Some seasonal migration by ringed seals (*Phoca hispida*) takes place (in the western Arctic; Smith 1987), largely by young-of-the-year, because of territorial exclusion by mature seals and competition for food. Except during the open water period, subadult seals tend to move considerable distances away from adult populations and congregate in separate areas (Smith 1976, 1973). Aside from such seasonal movements and reassortment of age classes, almost nothing appears to be known

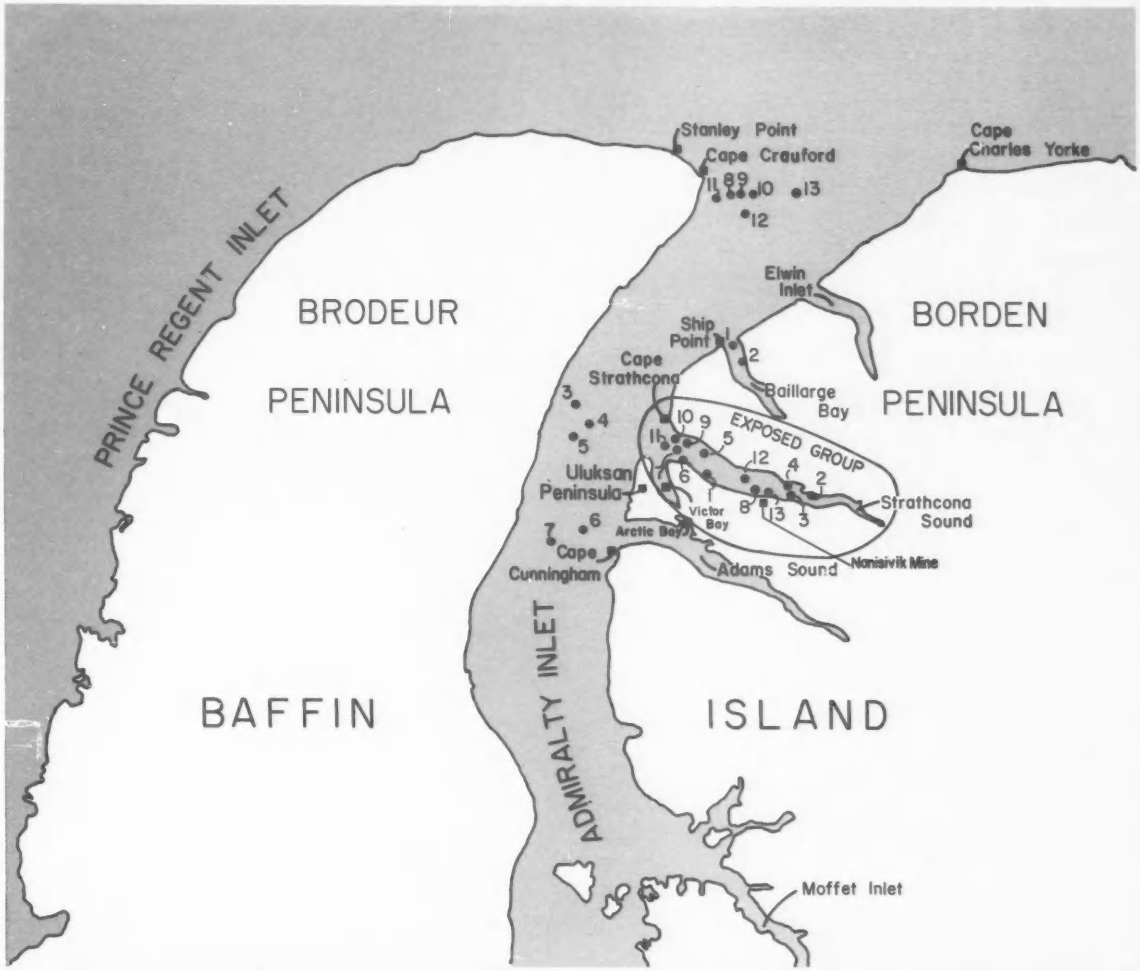

FIG. 1. Numbered positions indicate where individual seals were shot, the exposed group within the circled area, and the reference group outside the circled area. The Nanisivik mine site on Strathcona Sound is also indicated (within the circled area).

about the extent of travel under ice in search of food by these animals. According to McLaren (1958), the ringed seal is not truly migratory, and adults tend to be sedentary in areas delimited by fast ice of winter; immature seals are frequently found off-shore. Natives think (p. 72, McLaren 1958) that some seals return from year to year to the same winter residence. The movement or lack of it by these animals has implications for the uptake of pollutants from point sources.

The purpose of this study was to compare the concentration of some heavy metals in tissues of seals captured in the vicinity of the Nanisivik mine, with that in seals captured farther away from the mine site (Fig. 1), to see if significant differences exist between the two groups.

Materials and Methods

Sample Collection and Preparation

Ringed seals were collected in April and May of 1983, from two areas, the vicinity of the Nanisivik mine, and a relatively uncontaminated area approximately 50–75 km west of the mine area, Admiralty Inlet (Fig. 1). Animals from the latter area were used as a reference group as they were deemed sufficiently far removed from the mine site to avoid being directly affected by contamination from mining activities. The reference group consisted of 15 animals; (six males, nine females), two of which were pups taken from the same location as their mothers. The group from the vicinity of the mine, for the sake of convenience called the "exposed group," consisted of 13 animals (six males, six females, one unsexed). The location where each individual was shot is numbered on the map; the exposed group within the circled area, and the reference group outside the circled area (Fig. 1).

Animals were shot in the head by Native hunters. Unfortunately, ice conditions and the proximity of the animal to the water hole or water leads were not recorded. Tissue samples (liver, kidney, muscle), excised with a clean stainless steel knife, were placed in acid-cleaned polyethylene sample bags, frozen in the field, and shipped frozen to the Freshwater

Institute, Winnipeg, where they were kept at −40°C until analyzed. Prior to analysis tissue samples were thawed just sufficiently to be cut. An analytical sample was then excised from the interior of the bulk sample, cut into smaller pieces, weighed and placed in an acid-washed petri-dish, and dried for 16 h at 80°C to determine moisture. The dried samples were ground in a small coffee grinder, and stored in acid-washed plastic vials.

Chemical Analyses

The samples were analyzed for Cu, Cd, Pb, Zn, Hg, As, Se; for Cu, Cd, and Zn by flame atomc absorption, for Pb, depending on concentration, by flame or flameless atomic absorption, for Hg by cold-vapour atomic absorption, and for Se and As by semi-automatic flameless atomic absorption of their hydrides. The chemical procedures used, have been described in detail elsewhere (Wagemann et al. 1983; Armstrong and Uthe 1971; Vijan and Wood 1976). Preconcentration, by chelation with DDDC and extraction into *n*-butyl acetate, was required for Pb determinations, described previously in detail (Wagemann et al. 1983). Digests were buffered with citrate (pH 8.6) prior to extraction.

Triply distilled water (from a quartz still) was used to make up standards, samples, and reagents. For Pb in particular, low blank readings (≤0.04 Absorption) were ensured by purification of reagents and careful cleaning of glassware. Blanks and standard Bovine Liver #1577A NBS, U.S.A. were carried through the procedure in the same way as samples including, for the determination of Pb, the extraction of standards and blanks. The bovine liver was an unsuitable standard for Hg, and therefore a secondary reference material (fish muscle), calibrated in an inter-laboratory comparison was used for this metal. Agreement between analytical results for standards and their certified value was within 90% or better for all metals.

All samples were analyzed for a particular metal on the same day and by the same analyst, and the methods and analytical competence of the laboratory were confirmed in a separate international comparative study of trace metals (Cu, Cd, Zn, Pb, Hg, Se) in marine mammal tissue (Wagemann and Armstrong 1988, for details). Precisions for the various metals were (in terms of the coefficient of variation): 3–7% for Cu, Zn, Cd; 30% for Pb; 6% for Se; 5% for Hg. The precision of results from a single laboratory (including the Winnipeg Laboratory) was generally better than these values. The precision for As was estimated to be the same as for Se. Previous analytical data for a marine mammal from this laboratory had also been confirmed by an independent laboratory (Wagemann et al. 1983). Methods were unchanged in this study. Metal concentrations were expressed as micrograms per gram dry weight of sample. All statistical analyses were performed with data expressed on a dry weight basis.

Age Determination

Seals were aged by five blind replicate counts of dentinal annuli in thin sections of the lower left canine. The counts were averaged and confidence limits for the mean were calculated (95%). Counts outside this limit were not used. The final age in terms of years (using April 1, as the birth date), was the median reading of the remaining counts. Optimal use of clear sections was made (i.e. either longitudinal or cross sections were used (McLaren 1958; Smith 1973; Stewart and Lavigne (1979)). Neonates that had no erupted permanent teeth were assigned to the 0-yr age class.

Statistical Treatment

Multiple linear regressions were performed by the stepwise, backward procedure using all metals and age but not sex, since the groups were too small for inclusion of this additional variable. The analysis was repeated on each set using each variable in turn as dependent and independent. Correlations that were significant with a variable being both dependent and independent were accepted. A critical probability level of 0.90 was chosen for retention of a variable in the model. Regressions were carried out on log-transformed ($\ln(x+1)$) data. This transformation rather than $\log(x)$, was used to avoid problems arising with small numbers in the latter transformation.

In those cases where only one independent variable remained in the regression model, the confidence interval for a single future point at coordinate x on the regression line was calculated (at $\alpha = 0.05$) in the usual way:

$$\hat{y} \pm a(t_{1-\alpha/2,n-2})$$

$$a = s_{y/x}[1 + 1/n + (x_i - \bar{x})^2/(n-1)s_x^2]^{1/2}.$$

The symbols in the preceding formulas have the usual meaning. For the calculation of a confidence interval of a point on a regression surface, a more complicated version of the above formula was used (Snedecor and Cochran 1980, p. 351). The *t*-test was used ($\alpha = 0.05$) to compare two means.

Results and Discussion

Background Levels in Reference Group

Cadmium can vary greatly among individuals within a group of marine mammals from the Arctic as was found here (Table 1), and as reported previously (Wagemann et al. 1983). Three animals in the reference group had high Cd concentrations in the kidney; 379, 385, and 608 μg/g dry weight (109, 93, 128 μg/g wet weight). This precluded using this group as a reference for Cd. The highest hitherto reported mean Cd concentration for seal tissue was 267 μg/g (dry weight) in the kidney of a northern fur seal (*Callorhinus ursinus*) from the Pribilof Islands, Alaska (Goldblatt and Anthony 1983). Since the reference group was composed largely of mature animals, the dependence of Cd in kidney on age (Table 2), could account partly for such high values.

Mean As values were comparable with those in the same organs of the narwhal (Wagemann et al. 1983). Means for other metals were either not significantly different between the two groups (Se, Cd, Hg, Zn in liver; Zn in kidney; As in muscle), or were also higher in the older reference group than the exposed group (As, Cu in liver; As, Cu, Se, Cd in kidney; Cu, Cd, Hg in muscle), and all except Cd were within the range of values reported previously for seals or other marine mammals (Wagemann and Muir 1984).

Relation between Levels and Age in Reference Group

Strong associations among metals, and between metals and age were found in the reference group, notably a positive one between Hg and Se in the liver and between age and Hg and Cd in the kidney (Table 2). The Pb concentration in the three tissues examined was independent of age, but was positively correlated with Se in liver and negatively with Hg in kidney.

TABLE 1. Means of metals (microgram per gram dry weight), (SD), ranges, and percent moisture (*M*) in two groups of ringed seals.

	Liver		Kidney		Muscle	
Metal	Exposed	Reference	Exposed	Reference	Exposed	Reference
Pb	0.11	0.053	0.17	0.080	0.052	0.029
	(0.062)	(0.029	(0.43)	(0.059)	(0.038)	(0.022)
	0.21–0.50	0.11–0.020	1.58–0.020	0.20–<0.002	0.15–0.010	0.09–0.010
Se	13.91	20.5	7.65	9.35	1.64	1.49
	(22.15)	(13.9)	(1.85)	(1.25)	(0.24)	(0.19)
	65.9–2.40	46.3–3.02	12.0–4.92	11.5–7.27	1.94–1.25	1.78–1.25
Hg	23.6	28.4	4.22	5.56	0.49	1.07
	(52.3)	(21.6)	(2.65)	(2.88)	(0.36)	(0.47)
	173–0.89	70.9–2.29	11.3–2.08	12.4–1.51	1.23–0.14	2.48–0.61
As	0.71	1.69	0.36	1.31	0.13	0.19
	(0.97)	(0.69)	(0.43)	(0.899)	(0.096)	(0.20)
	3.04–0.05	2.63–0.53	1.49–0.05	2.60–0.06	0.30–0.05	0.73–0.05
Cd	11.93	33.2	76.7	208	0.189	0.409
	(12.73)	(20.8)	(82.9)	(167)	(0.182)	(0.213)
	39.4–1.00	66.6–1.00	222–2.00	608–2.00	0.63–0.05	0.78–0.05
Cu	35.41	64.3	38.7	27.2	8.56	6.92
	(25.78)	(96.8)	(19.7)	(12.1)	(2.53)	(1.56)
	84.1–12.4	370–12.4	178–15.2	64.9–12.7	11.7–4.68	10.2–5.20
Zn	171	182	216	203	82.9	75.2
	(52.9)	(112)	(54.5)	(81.6)	(20.2)	(22.8)
	287–121	576–122	356–120	441–104	134–57.6	135–52.0
M	70.0	69.2	75.4	76.4	70.1	70.2
	(1.8)	(3.0)	(1.8)	(2.1)	(1.6)	(2.1)
	73.6–67.1	76.2–65.1	78.7–73.1	79.5–71.2	73.6–67.8	75.2–67.6

TABLE 2. Associations between metals As, Se, and age, in liver kidney, and muscle of the AB-group of seals at $0.90 \leq P \leq 0.95$, $0.95 < P \leq 0.99$*, and $0.99 < P$**. The direction of the regression slope is indicated by the algebraic sign before the chemical symbol.

	Independent variables		
Dependent variable	Kidney	Liver	Muscle
Cd	+Age**, +Zn**, +As**	−Cu*	−Zn**
Cu	−Age**, +Zn*, +As*	−Age**, −Cd	−Age*
Zn	+Cd**, +Cu**	+Cu*, −Se	−Age*, −Cd*
Pb	−Hg	+Se*	—
As	+Cd**, +Cu*	+Age	—
Se	—	+Hg**, −Zn	—
Hg	+Age**	+Se**	—

Copper in all three tissues was negatively correlated with age. Similarly, As and Zn in muscle were negatively correlated with age. Previous investigators have reported a similar positive correlation between Hg and Se in marine mammals (Koeman et al. 1973; Wagemann et al. 1988), between age and Hg and Cd (Roberts et al. 1976; Muir et al. 1988), and a negative correlation between age and Cu in other marine mammals (Wagemann et al. 1983). Arsenic in the liver was positively correlated with age.

In the exposed group of animals (mine area), probably as a consequence of their narrow age distribution, associations between metals and age were mostly lacking, except for the negative one between age and Cu, but this was heavily influenced by the three mature individuals in this group. However, such a negative correlation, indicating a decrease of Cu concentration with age has been observed previously in very young animals (Wagemann et al. 1988; Lui 1987; Honda et al. 1983), and appears to be a general occurrence in mammals after birth.

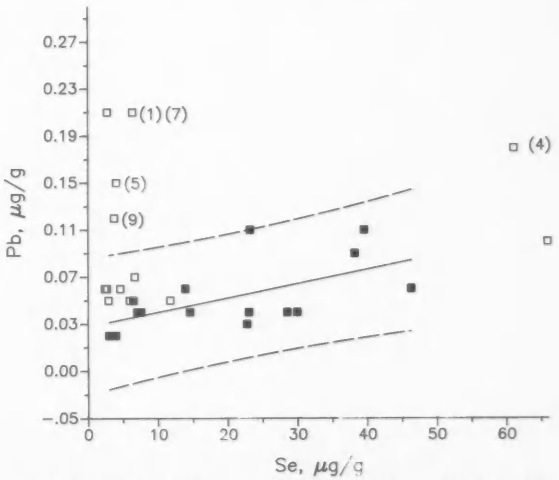

FIG. 2. Regression of reference group lead data (■) on Se in liver (dry weight basis) with 95% confidence bands, and exposed group data (□) superimposed. Concentrations above the upper confidence limit (exposed group data) are deemed to be significantly higher than the reference group data. Numbers in parentheses beside data points refer to capture locations in Fig. 1.

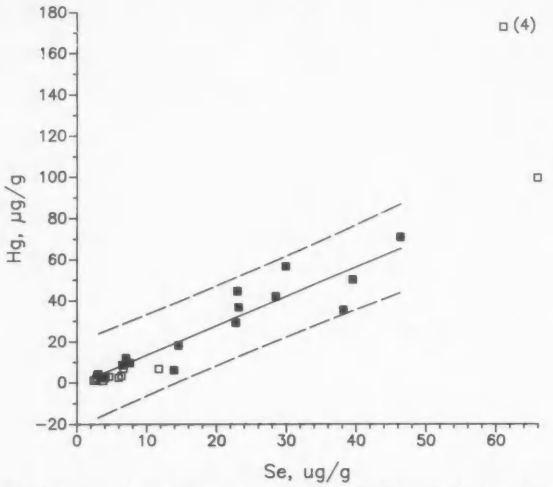

FIG. 3. Regression of reference group Hg data (■) on Se in liver (dry weight basis) with 95% confidence bands, and exposed group data (□) superimposed. Concentration point (4) (exposed group data) is much above the upper confidence limit and deemed abnormally high.

Of what importance or detriment this might be to the animals is not known.

Comparison of Exposed and Reference Groups

The question in the present study was whether or not apparently high individual metal values (particularly Pb) were within the norm for ths geographic area and age group. All except three animals in the exposed group (8, 15, 22 yr) were <2 yr old, while the age distribution of the reference group was much wider (<0.6 to 18 yr, 8.2 yr mean). Yet the mean Pb concentrations in liver and muscle, and Se in muscle (Table 1) were significantly higher ($\alpha = 0.05$, *t*-test) in the exposed than in the reference group. Although the mean Pb concentration in kidney was also higher in the exposed than the reference group, statistically there was no difference between the two groups because of a large variation among individuals of the exposed group.

To account in the comparison for possible correlations between various metals themselves, individual values of the exposed group were compared with the regression line (or regression surface) of the reference group. Concentrations of the exposed group (plotted on the same graph as reference values) were considered abnormally high when they exceeded the upper confidence limit (95%) of the regression line for the reference group (Figs. 2 and 3). By this criterion, nearly half of all the captured animals in the exposed group had high Hg, Cd, or Pb concentrations in the liver or the kidney (data not shown) compared with the reference. Normally, old animals are expected to have higher heavy metal concentrations (e.g. Hg, Se, Cd) in tissues than young ones (Goldblatt and Anthony 1983; Wagemann et al. 1983, 1988).

The high values in the exposed group were almost certainly of biological and not analytical origin. The verification of the quality of analytical data had been undertaken before and after this study (Wagemann et al. 1983; Wagemann and Armstrong 1988). Exposed animal No. 13, captured closest to the mine site (Fig. 1), had the highest Cd concentration in the exposed group (222 µg/g dry weight, 49 µg/g wet weight), and the highest Pb concentration in the kidney (1.58 µg/g dry weight, 0.35 µg/g wet weight) of all the captured animals. This was a high concentration of Pb to be found in soft tissue and may indicate recent intake of Pb by this animal. Lead accumulates over the long term preferentially in bony tissues. Narwhal from the Canadian Arctic had only an average of 0.018 µg/g, wet weight, Pb in the kidney (Wagemann et al. 1983). Similarly high Pb values have only been reported previously for grey seals (Holden 1975) and harbour seals (Roberts et al. 1976) from European waters. Pinnipeds from coastal waters of highly industrialized or densely populated land masses are known to be burdened with heavy metals and other pollutants (Reijnders 1980; Van de Ven et al. 1979; Kari and Kauranen 1978). Criticisms have however, been expressed of published lead data in general, which may limit the usefulness of such comparisons (Analytical Chemistry 1980), particularly since many such data were produced a decade or more ago with insufficiently stringent methods (Burnett and Patterson 1980). Comparison of the test group with a reference group from the same general area, and analysis of both groups by the same laboratory and the same method, as was done here, greatly minimizes variations in the analytical quality of the data being compared. For Pb, such comparisons may therefore be more reliable than comparisons with older literature data. Some metals data for ringed seals from the Strathcona Sound area for the period prior to the commencement of operation of the Nanisivik Mine are available (B. Fallis, unpubl. data, cited in Wagemann and Muir 1984), but are of limited usefulness here because the three metals of most interest (Pb, Cd, Hg) were either not measured (Pb, Cd in kidney) or were determined only as upper limits. Only Cd in liver is available as a comparative value, but this organ is not the preferred site for long-term Cd accumulation.

Arsenic in liver and kidney was significantly higher in the reference than the younger, exposed group. This was likely a reflection of the older age of the reference group compared with the exposed group. In the kidney there was no strong correlation between As and age that might explain the relatively higher values.

Possible Source of Contamination

Since the exposed group, notwithstanding their relatively young age, had a significantly higher mean Pb concentration in liver and muscle than the reference group (Table 1), local Pb pollution appears to have contributed to their Pb burden. The occurrence of relatively high concentrations of Pb, Zn, Cd, and As in seaweed, molluscs, and sediments in Strathcona Sound in the vicinity of the marine terminal of the Nanisivik mine and its ancillary installations was reported by Fallis (1982). A positive correlation of metal concentration in animals collected at decreasing distances from the point source was not found. The complexity of water currents in Strathcona Sound, which are undoubtedly as complex here as in other fjords with tidal influences and the movement of seals, presumably prevented a simple relationship between distance and concentration. It is noteworthy that a 1-yr old, shot closest to the mine site, had the highest Pb and nearly the highest Cd concentration in the kidney of all animals.

In the case of Cd, factors such as metals-enriched foods in the eastern Arctic generally, may have been more important than local pollution. Norstrom et al. (1986) found a general trend of increasing Cd in livers of polar bears from the western to the eastern Canadian Arctic. Macdonald (1986) analyzed die-

tary items of ringed seals (invertebrates, fishes) from three locations in the eastern Arctic (Resolute, Cape Hatt, Arctic Bay) and found that the amphipods (*Parathemisto abyssorum, P. libellula*, and *Hyperoche medsarum*) had the highest Cd concentration of the various organisms analyzed. The extent of the contribution from this source to the Cd found in both groups of seals in this study, is an open question.

Conclusion

Marine mammals from the Arctic were not suspected of being burdened with metals until published data showed that some marine mammals had high concentrations of Cd (in seals from Alaska, Goldblatt and Anthony (1983), and whales, Wagemann et al. (1983)), and Hg (in seals, Smith and Armstrong (1978), and whales, Imperial Oil Limited (1978)) in their tissues. Cadmium in the kidney of seals from the Canadian Arctic had hitherto not been measured. This study shows that a group of seals from Strathcona Sound in the vicinity of the Nanisivik mine had higher Pb concentrations than a reference group from Admiralty Inlet. The work that has been done to date indicates that the Arctic is not as pristine as it once was thought to be. It is important to determine the frequency of occurrence of high metal values in marine mammals of the Canadian Arctic in order to obtain a better understanding of background levels of heavy metals in such animals and of dietary intakes of heavy metals from this source by coastal Natives.

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Effects of Heterogeneity in the Spatial and Temporal Pattern of Juvenile Alewife (*Alosa pseudoharengus*) and Blueback Herring (*A. aestivalis*) Density on Estimation of an Index of Abundance

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Jessop, B. M., and W. E. Anderson. 1989. Effects of heterogeneity in the spatial and temporal pattern of juvenile alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) density on estimation of an index of abundance. Can. J. Fish. Aquat. Sci. 46: 1564–1574.

Significant heterogeneity occurred in the spatial and temporal pattern of the nocturnal, near-surface (0 to 1.5 m depth) density of juvenile anadromous alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) in the Mactaquac Dam headpond, Saint John River, New Brunswick. Juvenile alewife were less available to a pushnet than were blueback herring. Patches of higher density persisted for up to 4 wk for both species. Estimates of patch size depended upon the sampling scale, with larger patches (16 to 58 km long) composed of smaller patches (0.5 to 2.2 km long). The index of aggregation of Taylor's power law was similar for both species (pooled value 2.20). Lloyd's index of patchiness varied significantly, for both species, spatially but not temporally, and tended to be higher for blueback herring than for alewife. Density and patchiness differed for both species within and between an upriver, lotic zone and downriver, lentic zone. Mean densities were more precisely estimated at high than at low densities and for alewife than for blueback herring ($n = 61$). Stratification increased the precision, relative to simple random sampling, of estimates of mean density, particularly at high densities of the more patchily dispersed blueback herring. Autocorrelation occurred in the spatial density pattern of both species at coarse (1–100 km) and medium (0.1–4 km) sampling scales. Variations in the intensity and grain of patchiness may affect the choice of survey design, sample and sample unit size, and frequency of sampling required for a desired precision of density estimates.

On a relevé une hétérogénéité considérable dans les configurations spatiales et temporelles de la densité nocturne près de la surface (0 à 1,5 m de profondeur) du gaspareau (*Alosa pseudoharengus*) et de l'alose d'été (*A. aestivalis*) juvéniles anadromes dans le bassin principal du barrage Mactaquac dans la rivière Saint-Jean au Nouveau-Brunswick. Les jeunes gaspareaux étaient plus difficiles à capturer à l'aide d'un haveneau que les aloses d'été. Des taches de densité supérieure ont persisté jusqu'à 4 sem pour les deux espèces. Les estimations de la taille de ces taches dépendaient de l'échelle d'échantillonnage, les taches les plus importantes (16 à 58 km de longueur) étant composées de taches plus petites (0,5 à 2,2 km de longueur). L'index d'agrégation de la loi de puissance de Taylor était semblable pour les deux espèces (valeur groupée 2,20). L'indice de répartition par taches de Lloyds variait considérablement pour les deux espèces sur le plan spatial, mais non sur le plan temporel, et tendait à être plus plus élevé pour l'alose d'été que pour le gaspareau. La densité et la répartition par tache des deux espèces différaient à l'intérieur d'une zone lotique du cours supérieur des cours d'eau et d'une zone lentique en aval, ainsi qu'entre les zones. Les densités moyennes ont été estimées de façon plus précise à densité élevée qu'à densité faible; les estimations étaient également plus précises dans le cas du gaspareau que dans celui de l'alose d'été ($n = 61$). La stratification augmentait la précision, par rapport à un simple échantillonnage aléatoire, des estimations de la densité moyenne, particulièrement aux fortes densités des aloses d'été, davantage dispersées en taches. Une autocorrélation a été établie dans la configuration de densité spatiale des deux espèces aux échelles d'échantillonnage grossière (1–100 km) et moyenne (0,1–4 km). Les variations de l'intensité et du grain de la répartition par taches pourraient influer sur le choix du plan de relevé, de la taille de l'échantillon et de l'unité d'échantillonnage, et de la fréquence d'échantillonnage nécessaire pour obtenir la précision désirée dans les estimations de la densité.

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No consensus exists on the causes or ecological effects of patchiness in aquatic systems aside from agreement that it results from complex interactions between biological and physical processes (Horwood and Cushing 1978; Richerson et al. 1978; Legendre and Demers 1984; Siler et al. 1986). Patchiness, as well as the sampling scheme design, can influence the accuracy and precision of abundance estimates, particularly if more than one species is surveyed (Platt et al. 1970; Haury et al. 1978; Koeller 1981; Leaman 1981; Koeller et al. 1986).

Spawning escapements of adult anadromous alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) are annually released to the Mactaquac Dam headpond, Saint John River, New Brunswick (Fig. 1). The returns support a major commercial harvest (1980–88 mean of 456 t), the management of which could be improved by an understanding of the links

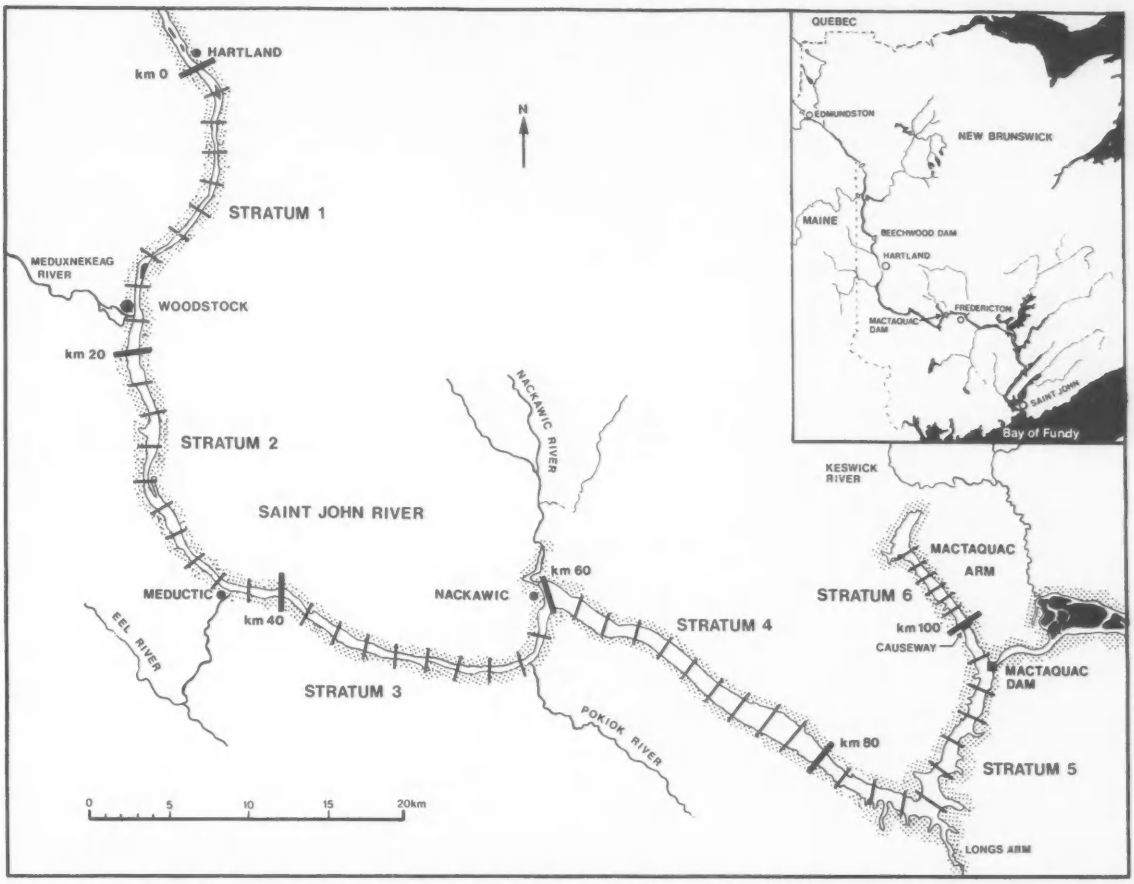

FIG. 1. Map of the Mactaquac Dam headpond, Saint John River, New Brunswick, showing survey stratification scheme.

between stock and recruitment. Trawl-based indices of juvenile abundance can be used as estimators of year-class strength and population trends (Koeller et al. 1986), for estimation of natural mortality rates (Zweifel and Smith 1981), for the calibration of sequential population analyses (Rivard 1981), or in a stock–recruitment relationship (Crecco et al. 1983), all of which are useful management tools.

This study measured the temporal and spatial variability in the pattern (or arrangement, as opposed to distribution in a statistical sense; Pielou 1974) and patchiness of sympatric juvenile anadromous alewife and blueback herring in a hydroelectric dam impoundment, tested whether differences existed within and/or among species in availability to the sampling gear, in temporal and spatial heterogeneity of density, and in the intensity (range of observed densities) and grain (dimensions of aggregations) of spatial pattern, then evaluated the effect of such variability on the design of surveys to estimate biological and population characteristics, particularly an index of abundance.

Study Area

The Mactaquac Dam headpond (Fig. 1) is about 106 km long, 87.3 km^2 in area, has a total storage volume of 1360×10^6 m^3, and epilimnion volume of 900×10^6 m^3 (Watt 1973). Seventy percent of the Saint John River drainage area (34 300 km^2) is upriver of the Mactaquac Dam, which is located 148 km from the river mouth. Low flow periods occur during summer and winter. The mean summer discharge (June–September, 1980–86) of 557 $m^3 \cdot s^{-1}$, drawn from depths of 8–21 m, may influence the thermocline width (5–10 m) and depth (≈20 m). Typically, the headpond level fluctuates <0.3 m daily, and <1.3 m weekly. A headpond bottom slope (≈0.36 $m \cdot km^{-1}$) produces water depths of about 40 m immediately upstream of the dam, 30 m at 50 km, and 4 m at about 100 km upstream (S. Ismail, New Brunswick Electric Power Commission, pers. comm.). The main stem of the headpond can be divided at Nackawic into an upper lotic region with a shallower depth (4–25 m), narrower width (0.3–0.7 km) and higher current velocity, and a lower lentic region with a greater depth (31–40 m), and width (1.0–1.5 km), and less current. The Mactaquac Arm is also a lotic region, with shallow depth (3–15 m) and moderate width (0.4–0.7 km).

Methods

The approximately 100 km long main stem of the Mactaquac Dam headpond upriver of the Mactaquac Arm causeway was divided arbitrarily into five strata each 20 km long and subdivided into 2-km substrata (Fig. 1), with the Mactaquac Arm

(which is partially isolated from the main headpond by a 0.4 km long causeway) forming a sixth stratum 6 km long with 1 km substrata, since little statistical benefit is gained from more than six strata (Cochran 1977). The final upriver substratum in the main stem and in Mactaquac Arm were excluded because of narrow width, shallow depth, or obstructions. Substratum widths were divided equally into three cells. The survey area thus contained 163 cells (148 in the main stem (147 plus one for Longs Arm), and 15 in Mactaquac Arm). Strata 1–3, 4–5, and 6 encompassed an upriver lotic zone, a lower lentic zone, and Mactaquac Arm, respectively containing about 35, 60, and 5% of the surveyed area.

All sampling for juvenile alewife and blueback herring was done on calm water during full darkness using a bow-mounted pushnet (1.5 × 1.5 m mouth) with 12.7-mm stretch mesh (Jessop 1985). All runs, unless otherwise noted, were for 5 min at a speed of 1.1 $m \cdot s^{-1}$ (confirmed by calibrated flowmeter) and covered approximately 330 m. Catch was adjusted to a standard volume of 700 m^3, hereafter referred to as CPUE (catch per unit effort) or density (synoptic survey mean volume filtered = 744 m^3; $n = 163$; CV (coefficient of variation) = 1.4%). All cells were sampled proceeding downstream from the uppermost stratum. Loran-C was used to position the boat within each substratum using previously determined coordinates (repeatability of about ±20 m); within-cell positioning was done visually relative to the shore.

Catches were preserved in 4% buffered formalin, then sorted and enumerated by species, usually within 5 d of capture. Alewife were distinguished from blueback herring following criteria in Lippson and Moran (1974), particularly peritoneal colour.

Among-species differences in nocturnal availability are not definitively answerable by surface gear studies. Comparison by Mann–Whitney *U*-test of the ratios of maximum seasonal geometric mean juvenile CPUE to adult escapement for the years 1982–88 was used as an indirect indicator of differential availability, given the assumption of similar juvenile survival by both species.

Nocturnal and latitudinal variability within species in density were assessed by three replicate runs made at each of three distances (total nine runs) from the shoreline and repeated through the night at 1.5 h after sunset (19:30), 1.5 h before sunrise (04:45), and midway between (01:30). Each triad of runs began 15–20 m offshore, and proceeded outwards (to 25 and 50% of the approximately 1 km width of the reach) and upriver in a stepwise manner. Illumination levels (lux) were measured at the start and end of each run series and the mean value used as an index. The site, opposite and upstream of Longs Arm, was chosen because of its width, roughly parallel shores, distance from major habitation, inflowing streams, the dam, and expected moderate fish densities.

Among- and within-species variability in medium scale spatial and nightly temporal density was examined by replicating three times a series of 32 contiguous, 1.5-min runs (quadrats) selected cells divided among strata in proportion to surface area and with a minimum of six cells per stratum. Consequently, the 0–19 km and Mactaquac Arm strata received a 50–85% higher-than-proportional allocation of sampling effort. All 163 cells were sampled for the third biweekly survey to evaluate the representativeness of the pattern in spatial density and of precision of stratum and stratified means relative to the standard 61-cell (selected in advance) survey. Water temperatures (degrees Celcius) were measured in 1-m increments from the surface to bottom or to 15 m depth at midstream at stations 10, 30, 50, 70, and 90 km downstream from kilometre 0, and centrally in Mactaquac Arm. Stratum mean CPUE's, the stratified mean, and 95% confidence intervals were calculated (Cochran 1977) for each biweekly survey.

Among-species differences in temporal and coarse scale spatial density value and pattern were evaluated by five biweekly, three times a series of 32 continguous, 1.5-min runs (quadrats) at 1.5 $m \cdot s^{-1}$. Runs proceeded upriver in midstream from a site just upriver of Longs Arm. Loran-C coordinates recorded at the start and end of each run (the end of a run became the start of the next) during the first replicate were repeated for subsequent replicates, in conjunction with time and speed measurements. Catch was adjusted to catch·135 m^{-1} (mean quadrat length = 131 m; CV = 0.9%).

Relationships examined by one- or two-way ANOVA included variation in: (1) density of each species, in relation to nocturnal sampling time and location (relative to headpond width), (2) stratum mean CPUE's of each species within and among biweekly survey periods, (3) mean CPUE by species and stratum groupings (lotic, 0–59 km and lentic, 60–99 km), (4) stratified mean CPUE among survey periods, with sample sizes based on the effective degrees of freedom ($n = df + 1$) as estimated by Satterthwaite's approximation (Cochran 1977), (5) CPUE among quadrats and survey nights for each species.

All catch values were transformed ($\log_{10}(X+1)$) for statistical analysis; reported mean catches are geometric means back-transformed by exponentiation and subtraction of the constant. The basic assumptions underlying the use of fixed effects model ANOVA (Sokal and Rohlf 1981) were examined whenever feasible, and unless otherwise mentioned, are believed to have been satisfactorily met. The duration of sampling within a survey period was assumed minor relative to the time required for a significant change in the among-strata spatial pattern of juvenile fish and fish densities within a cell were assumed homogeneous. Statistical significance was accepted at the $P \leq 0.05$ level.

Spatial dispersion within the headpond was further examined using Taylor's power law $s^2 = am^b$ relating the variance (s^2) and mean (m) catch by a power function (Perry 1981). The exponent b is considered a species-specific index of aggregation and may vary continuously from zero for a regular pattern to infinity for a highly contagious pattern although it usually is <4; a depends mainly on the size of the sampling unit and on the environment (Taylor et al. 1978; Taylor and Woiwood 1982). Functional (geometric mean; *GM*) regressions of the logarithm (base 10) of the variance (Y) on the logarithm of the arithmetic mean ($n = 3$; in one case 4) substratum catch (X) from the third biweekly synoptic survey ($n = 163$) were used to estimate the a and b coefficients for each species (Perry 1981; Taylor and Woiwood 1982). Ordinary least squares regression was used to compare slopes with the conclusions likely applicable to the *GM* case when the correlation coefficients are high (Jensen 1986).

Patchiness (p) or pattern intensity for each species was estimated, in terms of the crowding of an individual relative to the average crowding in a randomly dispersed population, by Lloyd's index:

$$p = 1 + (s^2 m^{-1} - 1)\, m^{-1}$$

where m = the mean density of juvenile fish per stratum or sample of quadrats and s^2 = the associated variance (Lloyd 1967; Pielou 1977). Lloyd's patchiness index is theoretically inde-

pendent of density and sample unit size (Pielou 1977), thereby allowing comparisons of patchiness as density changes spatially or seasonally, and of patchiness values from surveys where sample unit size varies. The actual relationship between patchiness and sample unit size is unknown (McGurk 1986).

The assumption of a negative binomial count distribution by the index of patchiness was avoided by using the jackknife procedure to obtain robust and less-biased estimates of the index and associated confidence intervals (Reed 1983). The patchiness and mean crowding statistics were $\log_{10}(X+1)$ transformed prior to jackknifing. Transformed values of patchiness were compared by paired t-test using an experimentwise error rate (Sokal and Rohlf 1981).

Interactions between species were examined by the association measure W, as estimated by the two-way ANOVA method proposed by McCulloch (1985).

Cumulative sum (CUSUM) techniques, which detect changes in level within a time series and graphically summarize their magnitude and location (Woodward and Goldsmith 1964; Nicholson 1984), were used to estimate patch size in the density patterns of each species. Changes in the underlying mean of the series and, equivalently, the slope of the CUSUM were examined by the span test, which measures the maximum difference in density (V_{max}) occurring within a distance segment in which a change in mean is suspected. The test statistic V_{max}/s, where s is the sum of the root mean square deviation of adjacent observations in the time series, was compared with critical values (5% probability level) given by Nicholson (1984) for spans of different length. Patch size was determined by the number of contiguous substrata or quadrats having a similar positive slope of the CUSUM.

Results

Availability

Comparison over 6 yr (Mann–Whitney U-test) of the ratios of maximum seasonal geometric mean juvenile CPUE to adult escapement, for each species, indicated a significantly ($P<0.01$) higher ratio for blueback herring than for alewife (0.27 versus 0.03, respectively). This might mean either that blueback herring survive more successfully in the headpond, relative to spawning escapement, than do alewife or that differential vertical migration makes blueback herring relatively more available to the sampling gear. Since the 1986 alewife escapement was seven times that of blueback herring (1 131 000 versus 162 000) and total adult returns per spawner are roughly similar for both species (B. M. Jessop, unpubl. data), we conclude that blueback herring are more available to the gear than are alewife.

Temporal and Spatial Heterogeneity

Nocturnal density

Nocturnal mean densities (fish·700 m^{-3}) of alewife (101 at 22:30, 84 at 01:30, and 75 at 04:45) did not vary by time ($F_{2,18}=0.52$; $P>0.60$) or by location (or water depth) in relation to headpond width (86 inshore (5.2 m), 98 at 25% width (12.7 m), and 76 at 50% width (21.4 m); $F_{2,18}=0.39$; $P=0.68$). Blueback herring densities decreased slightly between dusk and dawn (from 199 to 128 to 90 fish·700 m^{-3} at 22:30, 01:30, and 04:45, respectively; $F_{2,18}=3.75$; $P=0.044$) but did not vary across the headpond width (141 fish·700 m^{-3} inshore, 121 at 25% width, and 135 at 50% width; $F_{2,18}=0.15$; $P=0.86$). Illumination levels at 1-m depth ranged from 25 to 40 lux. Interaction between treatment effects (time, location) was nonsignificant for catch of both alewife ($F_{4,18}=0.33$; $P>0.85$) and of blueback herring ($F_{4,18}=0.17$; $P>0.95$).

Significant changes in mean density (CPUE) occurred among weeks and strata for juvenile alewife ($F_{4,275}=52.1$, $F_{5,275}=17.6$, respectively; $P<0.001$) and for juvenile blueback herring ($F_{4,275}=49.0$, $F_{5,275}=28.9$, respectively; $P<0.001$) caught in the Mactaquac Dam headpond over the July 15 to September 9 sampling period in 1986 (Table 1). For both species, density was low in mid-July, peaked in late July or early August, and declined thereafter to a low value by early September. Mean water temperatures followed a similar pattern, increasing from 18.3°C in mid-July to 21.9°C in late July, then declining steadily to 16.5°C in early September. Stratified mean densities were similar ($P>0.05$) on July 28–29 and August 11–16 for alewife and on August 11–16 and August 25–26 for blueback herring.

Over the study period, systematic changes occurred in the longitudinal density pattern of both juvenile alewife and blueback herring in the main stem of the headpond (Table 1; Figs. 2 and 3). These changes were uncorrelated with water temperatures, which irregularly varied <1°C along the length of the headpond. Coarse scale patches of about 4 to 12 km in length occurred for both species at varying locations and times. Thus, the moderately dense patch of alewife that occurred between about kilometre 20 and 26 during late July was gone by mid-August but the concentration between kilometre 50 and 60 held for about 4 wk. The patch of alewife between kilometre 60 and 100 during late July appears to have moved downstream to kilometre 86–100 by mid-August and to have dissipated by late August. The high density patch of blueback herring located between kilometre 20 and 46 during late July also seems to have moved downstream to about kilometre 76 to 100 by mid-August, where it remained through late August while declining in density. The sharp increase in CPUE of blueback herring between mid- and late July may be linked with the concurrent decrease in overall mean length as an artifact of interaction between the sampling gear and changing fish catchability.

Division of the headpond into a lotic, upstream region (strata 1–3, 0–59 km) ending at Nackawic (Fig. 1), and a lentic, downstream region (strata 4–5, 60–99 km) revealed seasonally changing, geographic differences in density among and within species. Alewife density was significantly higher downstream than upstream prior to mid-August after which densities were about equal in both regions (Table 2). Blueback herring density was higher upstream than downstream during, and probably prior to, late July after which densities were higher downstream. Alewife and blueback herring densities upstream were similar in all sample periods except August 11–16, when blueback herring density declined sharply. Downstream, alewife densities exceeded those for blueback herring until mid-August when the density of blueback herring increased markedly, coincident with the decline in upstream density, after which it remained high through August. Significant ($P<0.001$) species × strata interaction effects occurred during the July 28–29 and August 11–16 surveys when densities of each species were highest and spatial patterns most different. Both species were relatively more abundant in the downstream region because of the higher densities and greater area downstream.

Significant differences in density of both juvenile alewife and blueback herring also occurred among quadrats along a contiguous, medium scale transect (density range 0–29.6 fish·135 m

TABLE 1. Geometric mean[a] catch·700 m^{-3} of juvenile alewife and blueback herring in the Mactaquac Dam headpond, Saint John River, 1986. For each species, means within columns (among strata) and stratified means among survey periods lacking a letter in common differ significantly from each other (ANOVA; $P \leq 0.05$). Intensive survey values are in parentheses (sample size, mean).

Species	River[b] (km) (stratum)	Sample size	Sample period				
			July 15–16	July 28–29	Aug. 11–15	Aug. 25–26	Sept. 8–9
Alewife	0–19(1)	6	0.0 z	7.8 z	12.7(27,13.2) zy	3.3 z	1.1 zy
	20–39(2)	8	0.6 z	11.3 zy	5.1(30,2.7) z	3.4 z	0.5 z
	40–59(3)	7	0.1 z	10.7 zy	16.1(30,15.8) y	19.1 y	7.9 x
	60–79(4)	19	1.4 z	19.8 zy	13.7(30,16.2) zy	12.0 y	4.2 yz
	80–99(5)	15	15.0 y	31.6 y	20.8(31,18.7) y	10.0 zy	2.3 zyx
	Mactaquac Arm(6)	6	1.5 z	7.8 z	16.9(15,9.3) y	6.9 zy	2.2 zyx
	Stratified mean	61	2.2 t	17.1 r	13.8(163,12.7) sr	9.1 s	2.7 t
	95% C.I.		1.5–3.3	13.6–21.4	11.1–17.1(11.0–14.6)	7.3–11.3	2.1–3.4
Blueback	0–19(1)	6	0.0 z	1.7 z	1.4(27,1.2) z	0.2 z	0.6 zy
	20–39(2)	8	0.0 z	22.7 x	3.2(30,2.3) z	5.5 y	0.3 z
	40–59(3)	7	0.1 z	13.6 yx	3.6(30,3.4) z	13.8 yx	4.1 yx
	60–79(4)	19	0.0 z	4.0 zy	18.0(30,14.0) y	9.9 y	5.6 x
	80–99(5)	15	1.9 y	3.3 zy	52.0(31,50.6) yx	37.3 x	3.5 yx
	Mactaquac Arm(6)	6	5.9 y	10.3 zyx	131.1(15,117.4) x	11.2 y	4.7 yx
	Stratified mean	61	0.5 t	5.9 s	15.2(163,13.2) r	11.7 r	3.1 s
	95% C.I.		0.3–0.7	4.4–7.9	11.1–20.7(10.8–16.0)	9.3–14.7	2.3–4.1

[a]Back transformed from $\log_{10}(X+1)$.
[b]Distance downstream from kilometre 0.

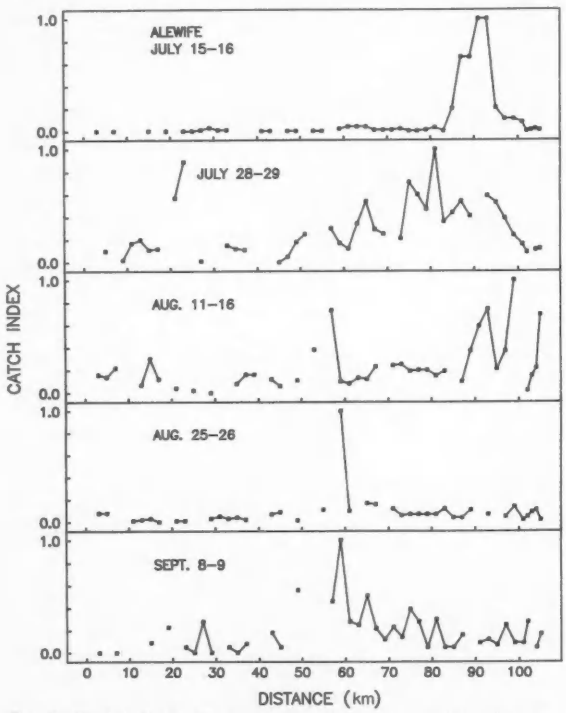

FIG. 2. Catch index (catch/maximum catch per survey) in relation to capture location (downstream of kilometre 0), by survey period, for juvenile alewife from the Mactaquac Dam headpond, Saint John River, 1986.

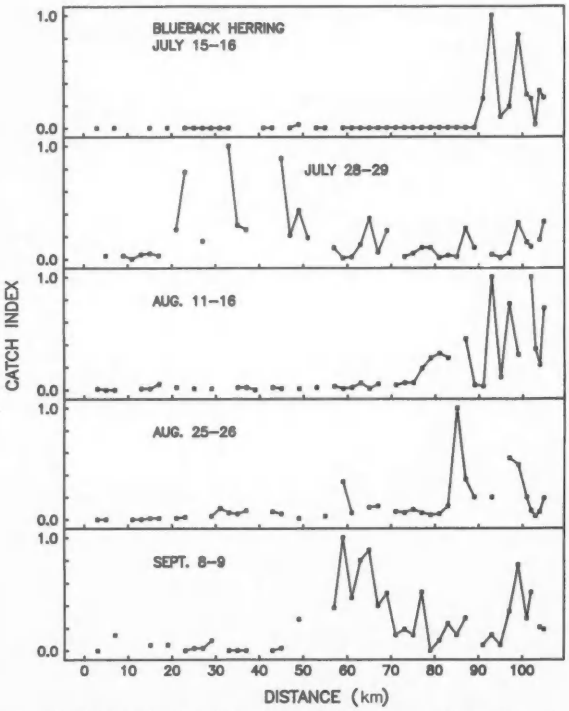

FIG. 3. Catch index (catch/maximum catch per survey) in relation to capture location (downstream of kilometre 0), by survey period, for juvenile blueback herring from the Mactaquac Dam headpond, Saint John River, 1986.

for alewife, 0–111.6 fish·135 m for blueback herring; $F_{31,62} = 16.7$ and 17.0, respectively; $P < 0.001$) and among closely spaced nights (density range of 0.9–4.1 fish·135 m for alewife, 6.0–17.0 fish·135 m for blueback herring; $F_{2,62} = 2.3$ and 3.9, respectively; $P < 0.005$) (Fig. 4). Coefficients of variation for quadrat catches ranged from 58–93% among nights for alewife and from 34–61% for blueback herring.

TABLE 2. Comparisons of the geometric mean[a] catch·700 m^{-3} of juvenile alewife and blueback herring, by strata and survey period, in the Mactaquac Dam hedpond, Saint John River, 1986. An asterisk indicates a significant ($P \leq 0.05$) difference between column or row paired means; df = 1,106 for F-test.

	Sample period									
	July 15–16		July 28–29		Aug. 11–16		Aug. 25–26		Sept. 8–9	
Strata (km)	Alewife	Blueback	Alewife	Blueback	Alewife	Blueback	Alewife	Blueback	Alewife	Blueback
0–59	0.3	0.0	10.0	9.8	9.8	2.6*	6.2	4.3	2.0	1.2
60–99	4.5	0.6*	24.4	4.7*	16.5	28.9*	11.1	18.0*	3.2	4.6
	*		*	*		*		*		*

[a]Back transformed from $\log_{10}(X+1)$.

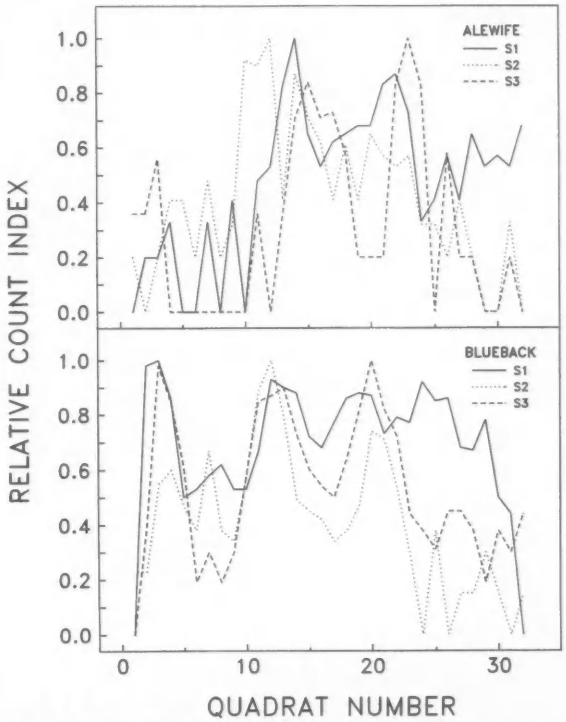

FIG. 4. Plot, by survey period, of the relative count ($\log_{10}(X+1)$ transformed) index (count/maximum count) of juvenile alewife and blueback herring catches on contiguous quadrat number, Mactaquac Dam headpond, Saint John River, 1986. Surveys (S) 1 to 3 were made on September 4, 6, and 7, respectively.

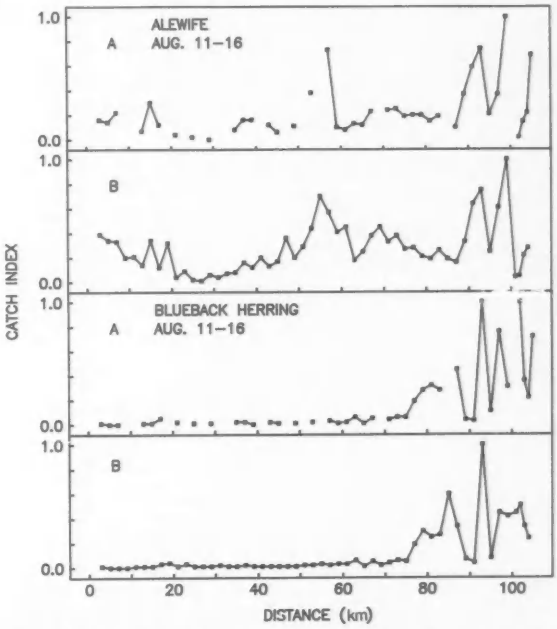

FIG. 5. Catch index (catch/maximum catch) in relation to capture location (downstream of kilometre 0), for juvenile alewife and blueback herring from the Mactaquac Dam headpond, Saint John River, 1986. For graph A, 61 of 163 possible cells were selected in a stratified random sampling scheme; all 163 cells were sampled for graph B.

Spatial Pattern, Intensity, and Grain

Variability in substratum (Fig. 5) and quadrat counts (Fig. 4), particularly for alewife, obscured the underlying pattern of spatial density, which CUSUM analysis revealed (Figs. 6 and 7). During the intensively sampled August 11–15 systematic survey, patches of alewife of medium density (13.5 and 17.3 fish·700 m^{-3}), and varying length (16 and 58 km) and position (kilometre 3–19 and 47–105) occurred along the headpond (Figs. 5 and 7). A single high density (63.3 fish·700 m^{-3}) patch of blueback herring 29 km long was found between kilometre 71 and 105. A single patch of alewife (1.6 to 1.9 km long) persisted in location along the 4.3-km transect during the fou. night period of the quadrat survey (Figs. 4 and 6). Size and location varied, in a manner suggestive of temporal and geographic persistence, for the two patches of blueback herring observed each survey. During surveys 1 and 3, patches of 0.5–0.7 km and 1.8–2.2 km length occurred, respectively, at the start and mid-way along the transect. During survey 2, adjacent patches of 0.5 and 1.2 km length occurred mid-transect.

The index of aggregation (b) of Taylor's power law, based on the GM regression, was estimated as 2.09 for juvenile alewife and 2.23 for blueback herring. The slopes of the corresponding predictive regressions (1.79 and 1.98, with $r^2 = 0.73$ and 0.79, and $n = 54$ and 53, respectively) were not significantly different (pooled value 1.93; $F_{1,101} = 0.60$; $P = 0.44$); thus, the slopes of the GM regressions are also unlikely to differ (pooled value 2.20).

Lloyd's index of patchiness varied significantly, for both species, among strata within a survey period but not among strata grouped into upriver (lotic) or downriver (lentic) regions, nor among survey periods (Table 3). In the survey of contiguous

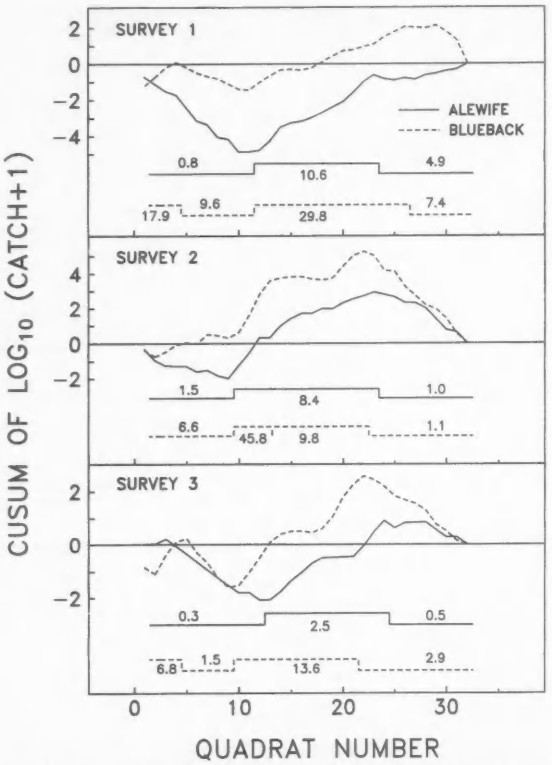

FIG. 6. Cumulative sum (CUSUM) plot of juvenile alewife and blueback herring catch ($\log_{10}(X+1)$ transformed) on contiguous quadrat number, Mactaquac Dam headpond, Saint John River, 1986. The Manhattan diagrams indicate patch size; numbers are mean densities. Surveys 1–3 occurred on September 4, 6, and 7, respectively.

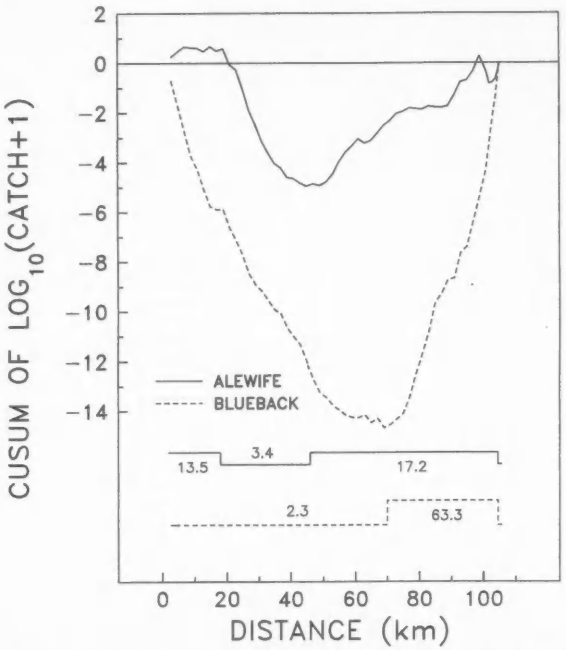

FIG. 7. Cumulative sum (CUSUM) plot of juvenile alewife and blueback herring catch ($\log_{10}(X+1)$ transformed) on capture location (downstream of kilometre 0), Mactaquac Dam headpond, Saint John River, 1986. The Manhattan diagrams indicate patch size; numbers are mean densities.

quadrats, the index of patchiness varied among nights for blueback herring but not for alewife. Within a night, the index did not vary for either species, and was similar for both ($n=9$; alewife range 1.1–1.4; blueback herring range 1.0–2.5).

Juvenile alewife and blueback herring were not associated, according to the association measure W, in either the upriver stratum group (Strata 1–3; $n=87$, $W=97$, critical values 72–102) or the downriver stratum group (strata 4–5; $n=61$, $W=62$, critical values 48–74), but were positively associated in the headpond as a whole (strata 1–5; $n=148$, $W=187$, critical values 128–167).

Statistical Considerations

At moderate juvenile fish densities (stratified geometric mean CPUE of 15–17), stratification increased the precision of the mean CPUE ($n=61$), relative to simple random sampling, by 33% for alewife and 132% for blueback herring; at low fish densities (stratified geometric mean CPUE of 3) precision increased 63 and 49%, respectively. At higher fish densities, stratification enabled estimation of mean CPUE within ±7–9% (95% probability level); at low fish densities, the precision decreased to ±13–15% of the mean. Precision was higher for alewife at both high and low densities. Among-weeks comparisons of stratified and unstratified mean densities were similar ($P>0.05$) in all but one of 10 cases.

Increased sampling frequency ($n=163$) had little effect (Table 1) upon estimates of stratum and stratified mean CPUE of juvenile alewife and blueback herring or upon evaluation of the density pattern within the headpond obtained from the biweekly sampling program ($n=61$). The intensive synoptic survey gave more precise estimates of the means, as judged by the narrower confidence intervals, but the coefficients of variation were similar for both sampling intensities (Table 4). For each species, the patterns of fish density in the headpond determined from both sampling intensities were virtually identical (Fig. 5).

The significant correlation ($P<0.01$) between catches in adjacent 2 km long substrata of the synoptic survey ($n=49$, excluding Mactaquac Arm) decreased with increasing lags of 2 to 8 km for alewife ($r=0.70$ to 0.47, respectively) and lags of 2 to 10 km for blueback herring ($r=0.77$ to 0.54, respectively). Autocorrelation of catches in 32 adjacent 135-m long quadrats decreased significantly from a pooled (over three replicates) mean correlation coefficient of 0.59 ($P<0.01$) to 0.49 ($P<0.05$) to 0.32 ($P>0.05$) at lags of one to three for alewife, and from 0.55 ($P<0.01$) to 0.19 ($P>0.05$) at lags of one to two for blueback herring.

For a sample size of 61, the power of a test ($1-\beta$) was sufficient (0.89) to reliably detect a 20% difference between biweekly stratified mean alewife densities at a 5% significance level, but was less satisfactory (0.64) for blueback herring. A 10% difference between means could not be reliably detected for either species.

Discussion

In any survey, the sample statistics representing population parameters depend upon the sampling gear and the survey

TABLE 3. Estimates of Lloyd's index of patchiness[a] and 95% confidence interval (C.I.), by stratum and stratum grouping for the synoptic survey and by run series for the quadrat survey, for juvenile alewife and blueback herring from the Mactaquac Dam headpond, Saint John River, 1986. Index estimates within a grouping without a letter in common are significantly different ($P \leq 0.05$); differences among species are indicated by an asterisk.

		Alewife		Blueback	
Grouping	*n*	Index	95% C.I.	Index	95% C.I.
Period			Synoptic survey		
July 28–29	61	1.76 z	1.51–2.04	—	—
Aug. 11–15	61	1.84 z	1.48–2.25	6.63 z*	2.50–15.65
Aug. 25–26	61	1.44 z	1.27–1.63	3.10 z*	2.25–4.16
Sept. 8–9	61	1.97 z	1.47–2.58	2.60 z	1.82–3.60
Stratum (km)					
0–19	27	1.27 z	1.11–1.44	4.05 z*	2.22–6.93
20–39	30	2.50 zy	1.47–3.95	3.43 z	0.83–9.75
40–59	30	1.59 zy	1.27–1.94	1.80 zy	1.22–2.54
60–79	30	1.40 zy	0.97–1.92	2.68 z*	2.07–3.40
80–99	31	1.76 y	1.48–2.06	3.82 zy	1.49–8.35
Mactaquac Arm	15	3.47 zy	1.14–8.32	1.28 y	1.10–1.47
0–59	87	1.86 z	1.52–2.24	2.56 z	1.92–3.33
60–99	61	1.63 z	1.41–1.88	5.21 z*	1.95–12.04
Overall	148	1.87 z	1.64–2.13	6.55 z*	3.18–12.63
			Quadrat survey		
Run series					
1	32	1.92 z	1.26–2.77	1.42 z	1.20–1.66
2	32	2.58f z	1.83–3.54	4.30 y	2.08–8.10
3	32	1.62 z	1.02–2.38	1.99 zy	1.53–2.55

[a]Index of patchiness estimates calculated only for periods of, and following, maximal CPUE for each species.

design. The assumption that juvenile alewife and blueback herring are equally available to a surface push-net is unjustified, consequent to a nocturnal difference in vertical separation (Loesch 1987; this study). Differences among species in availability to the sampling gear and failure to sample depth precludes estimates of population abundance but permits estimates of relative density if the availability of each species remains constant. Evaluation of the nocturnal spatial and temporal pattern of these species should be unaffected. Daytime sampling at depth might produce spatial density patterns different from those derived from near-surface sampling at night due to behavioural change by juvenile *Alosa* from diurnal schooling to nocturnal dispersal (Emery 1973; Loesch 1987). The assumption that the availability or proportion of each species that enters the catchable zone (0–1.5 m depth) is constant within and among survey periods is biased to the extent that relative availability to the gear differs seasonally among size groups due to ontogenetic behaviour and/or migration (Burbidge 1974; Janssen and Brandt 1980). Such bias is believed insignificant in this study because only juveniles having a limited size range are considered and data from different surveys are not pooled unreasonably. Similar densities throughout the night for each species support the assumption of constant nocturnal availability within a survey period. The further assumption that catchability (retention by gear and avoidance by fish) of the target organism by the gear remains constant within and among survey periods was not met to the extent that fish, particularly blueback herring which spawn later than do alewife, occurred smaller than about 27 mm fork length (30 mm total length) during early season sampling (Loesch et al. 1982; Jessop 1985).

Changes in temporal density and in pattern of spatial density of juvenile alewife and blueback herring may reflect the interaction of increasing catchability as they grow to full vulnerability to the gear, decreasing abundance due to continuing natural mortality, and seasonal downstream migration to the sea, the timing of which reflects the earlier spawning of alewife than of blueback herring. Seasonal maximum fish densities occurred during late July or early August for alewife and early to mid-August for blueback herring (this study; B. M. Jessop, unpubl. data). Downstream migration within the headpond by juveniles of these species occurred from about late July, in conjunction with decreasing water temperatures, through early September until at least late October (this study; B. M. Jessop, unpubl. data); migration from the headpond probably began about mid-August and increased rapidly through early September. Similar observations were reported for juvenile alewife in a Rhode Island reservoir (Richkus 1975) and for blueback herring in the Connecticut River (O'Leary and Kynard 1986).

Seasonal densities of juvenile alewife and blueback herring were greatest in the lotic portion of the headpond between about kilometres 60 to 90, coincident with peak zooplankton biomass (Watt and Duerden 1973). Fish density patterns in lakes (Gascon and Leggett 1977) and in some reservoirs (Siler et al. 1986) have been linked to nutrient (and associated phyto- and zooplankton) gradients controlled by mesoscale (1–100 km) water motions (Legendre and Demers 1984). Seasonal discharge level is the most important factor affecting (inversely) phytoplankton and, indirectly, zooplankton abundance in the Mactaquac Dam headpond (Laberge 1975).

Large scale patches of juvenile alewife and blueback herring (6–58 km long) persisted for periods ranging from less than 2 wk to, occasionally, four wk while medium scale patches (0.5–2.2 km long) occurred within larger patches for several days. Awareness of patch characteristics (position, longevity, size, etc.) contributes to understanding the ecological significance of patchiness, which reflects the interaction of environmental variation, habitat preferences, and behavioural actions, e.g. predator–prey interactions, seasonal migration, and schooling that induce organisms to aggregate independently of hydrodynamic factors (Haury et al. 1978; Horwood and Cushing 1978; Resh 1979).

The index of aggregation (exponent *b* of Taylor's power law), was similar (2.2) for both juvenile alewife and blueback herring and was within the range (1.8–2.2) observed for many species of birds and insects (Taylor and Woiwood 1982), which suggests that spatial heterogeneity was no less variable within species than among species. The value of the exponent *b*, which indicates the change of spatial behaviour in response to changes in population density (Perry 1981), may largely derive from a stochastic interplay between population demographic characteristics and environmental heterogeneity (Downing 1986). The potential bias in calculating and comparing exponents was minimized by the relatively large sample size (>50) and similar levels of replication and ranges of *m* for each species (Downing 1986).

The intensity of spatial pattern at night, as measured by Lloyd's index of patchiness, varied little for either juvenile alewife or blueback herring over the survey period (age of fish), over large geographic areas, or among different habitats (lotic versus lentic), but high catch variability gave wide confidence intervals. Densities varied greatly, but patchiness is independ-

TABLE 4. Relative precision, based upon the coefficient of variation (CV) in percent, of stratum and stratified means ($\log_{10}(X+1)$ transformed) from the biweekly and synoptic surveys of juvenile alewife and blueback herring densities in the Mactaquac Dam headpond, Saint John River, 1986.

	Biweekly					Synoptic			
	Alewife		Blueback			Alewife		Blueback	
Stratum	*n*	Mean	CV(%)	Mean	CV(%)[a]	*n*	Mean	CV(%)	Mean	CV(%)
0–19	6	1.14	19	0.37	124	27	1.15	23	0.35	125
20–39	8	0.79	53	0.62	50	30	0.57	75	0.52	71
40–59	7	1.23	31	0.66	48	30	1.22	26	0.64	47
60–79	19	1.17	24	1.28	31	30	1.24	24	1.18	37
80–99	15	1.34	26	1.72	35	31	1.29	25	1.71	31
Mactaquac Arm	6	1.25	41	2.12	14	15	1.01	46	2.07	10
Stratified	61	1.17	29	1.21	37	163	1.14	32	1.15	44

[a]Corrected for small sample size as necessary (Sokal and Rohlf 1981).

ent of density (Pielou 1977). Patchiness tended to be greater for blueback herring than for alewife, at least for the more reliable large sample case. Patchiness varied with age for the larvae of some marine fishes (Hewitt 1981) but may stabilize for juvenile fish, which have more behavioural control over their environment. Mortality rates of pelagic, marine fish larvae varied with patchiness (McGurk 1986); juvenile fish may be similarly affected.

Density and patchiness differed, for both juvenile alewife and blueback herring, between upriver (lotic) and downriver (lentic) zones of the headpond. Upriver, density of alewife was higher than, or similar to, that for blueback herring and patchiness was similar; downriver, density and patchiness were greater for blueback herring than for alewife. The smaller patch size of blueback herring at medium scales indicates a finer grain to their pattern than for alewife. Such differences may reflect species-specific behaviour in response to physical and biological environmental conditions at different spatial and temporal scales (Legendre and Demers 1984).

Juvenile alewife were not associated with juvenile blueback herring, in the sense that the presence of one species makes the presence of the other more or less likely (Pielou 1974), even though both species co-occur throughout the headpond. Their "association" was therefore passive and occurred simply because environmental conditions were suitable for these sympatric species and both were released into the headpond. The co-occurrence of a less abundant species with a dominant species may afford some protection from predation to the less abundant species and enhance its survival (Frank and Leggett 1983). The positive inter-species association in the overall headpond, but not in the upriver or downriver zones, may be an artifact of systematic among-sample differences in density pattern such as occur in a patchy environment (McCulloch 1985). A lack of inter-species association implies minimal competition among these species for environmental resources, as was concluded by Watt and Duerden (1973).

Geographic pattern, horizontal and vertical migration, and patch characteristics are important factors in the design of sampling programs (Pielou 1977; Haury et al. 1978; Millard et al. 1985; Koeller et al. 1986). Frequent lack of such information (Shotton and Bazigos 1984) has led to widespread use of stratified random sampling schemes for multispecies fishery surveys, with effort allocated in proportion to stratum area (Pennington and Brown 1981; Byrne et al. 1981). This conveniently ignores seasonal variability in patchiness and fish mobility, thereby producing only modest gains, relative to simple random sampling, in precision of density estimates, particularly at low densities (Cochran 1977; this study). Stratification and proportional allocation also spreads the sampling over the study area, providing a better representation of pattern than might be obtained by simple random sampling.

Non-Gaussian variability in catch requires data transformation prior to using parametric analysis methods. Transformation inadequacy may induce higher type I error, particularly with small sample sizes, and confidence intervals may be misleading (Pennington and Grosslein 1978). The value (2.2) of Taylor's index of aggregation supports the choice of a logarithmic transformation for normalizing the juvenile count data (Elliot 1977).

The required sample size is a function of the size and desired precision of the mean and the degree of patchiness (Resh 1979). High variation in the longevity and density of patches requires more frequent and intensive sampling to obtain unbiased and precise estimates of the density and of the spatial and temporal pattern of a population. A low sampling rate for a patchy pattern may increase the variance and widen the range of mean densities declared statistically similar while an extended survey period could introduce systematic differences between synoptic survey stations (Therriault and Platt 1978). Estimation of mean density with a given precision required a larger sample of the more patchily dispersed blueback herring than of alewife, while both species required larger sample sizes at low densities. About 60 samples were sufficient to estimate the stratified mean density of both species, at high and low relative densities, within $\pm$10–15% of the mean, at a 95% probability level. Since a variable sample size is usually operationally impractical and analytically undesirable, the sample size should be sufficiently large that any expected reduction in precision will still produce acceptable error limits. Patchiness effects were such that a larger ($2.7\times$) sample size minimally changed the accuracy (relative) and precision of density estimates. High variability combined with small sample sizes for moderate to large strata could permit a few large catches to greatly influence the estimate of the stratified mean, making trends in fish density more difficult to examine. Spatial pattern was, however, accurately discerned from relatively few, well distributed samples. For a given sample size, a systematic rather than stratified sampling scheme may best evaluate pattern, barring the unlikely event that the sample selection interval coincides with a periodic trend in that pattern (Cochran 1977).

Patchiness and sample size effects on the estimation of population density continue during repeated sampling of a population, as when growth, mortality, and production rates are estimated (Resh 1979). Autocorrelated spatial and temporal densities underestimate variances and overestimate precision. Spatial correlation is more likely to be a problem than is temporal correlation, which can be reduced by less frequent sampling at the cost of potentially bypassing important events (Millard et al. 1985). Biweekly sampling appears to be minimal for estimating indices of juvenile alewife and blueback herring abundance. More frequent sampling might be more informative but must be balanced against the increased cost and time required to complete a survey. Spatial correlation increases the advantage of stratified random sampling relative to simple random sampling. The comparison of spatial and temporal differences in fish density by ANOVA may be seriously affected by increased type I error of the *F*-test resulting from violation of the assumption of independence of errors (Sokal and Rohlf 1981). Patchiness may also confound the assumption of a stationary series required by the autocorrelation coefficient, biasing it for ecological data (Sokal and Oden 1978). Since variance increases with mean catch, which also increases with density, and mean and variance increase with sample unit size (Jessop 1985), the density and patchiness of each species affects the choice of sample unit size for a desired precision of the mean. Among-species variability in patchiness at different scales requires a careful, perhaps different, choice of sampling scale for different species to avoid the possibility of aliasing the data (Richerson et al. 1978). Sample unit size should be smaller than the scale over which changes in mean density occur (Pielou 1977), which makes push-net techniques unsuitable at scales less than about 100 m.

Increasing the sample size or the efficiency of the estimation techniques may increase the precision of the abundance estimator but not its accuracy, which may be improved by averaging several surveys, if temporal variability is high (Pennington and Brown 1981). The seasonal maximal CPUE (which may be an average if two or more survey means are not significantly different) from a series of surveys may be a better estimator than the seasonal mean when ontogenetic migration from the survey area or seasonal changes in catchability due to growth might be of concern (Loesch and Kriete 1983). Patchiness, combined with low sample sizes, may undesirably reduce the power of a test to distinguish two means, thereby leading to erroneously averaged "nonsignificantly different" means and underestimation of the index of abundance.

In summary, the heterogeneity observed temporally and at different spatial scales in the pattern of juvenile alewife and blueback herring density has substantial implication for the design and interpretation of studies of their biological responses to hydrodynamic processes, on our understanding of their life history, and ultimately on their management as a commercial resource.

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Influence of Rainbow Trout (*Oncorhynchus mykiss*) on Density and Feeding Behaviour of a Perlid Stonefly

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Feltmate, B. W., and D. D. Williams. 1989. Influence of rainbow trout (*Oncorhynchus mykiss*) on density and feeding behaviour of a perlid stonefly. Can. J. Fish. Aquat. Sci. 46: 1575–1580.

Stonefly (*Paragnetina media*) density was reduced in a rainbow trout (*Oncorhynchus mykiss*) enclosure by approximately 35%, whereas in a trout exclosure no significant changes in density occurred. Of the 35% reduction, approximately two-fifths and three-fifths were attributable, respectively to direct consumption of stoneflies by trout, and emigration by stoneflies from the predator-stressed section of stream. With trout present in laboratory aquaria, predator avoidance behaviour resulted in stoneflies remaining significantly more on dark substrate on which they were less vulnerable to trout predators. Stoneflies consumed significantly fewer prey (enchytraeid whiteworms) over 24 h, in the presence of both small (2.0–4.0 cm) and large (10.0–12.0 cm) rainbow trout in aquaria, compared with stoneflies feeding in trout-free aquaria. Feeding rate and substrate selection did not differ between well-fed and starved (5 d) nymphs.

La densité des perles (*Paragnetina media*) a été réduite d'environ 35 % dans une enceinte de truites arc-en-ciel (*Oncorhynchus mykiss*) tandis que dans une zone réservée pour la truite, aucun changement de densité significatif n'est survenu. Environ les deux cinquièmes et les trois cinquièmes de cette réduction de 35 % étaient attribuables respectivement à la consommation directe des perles par la truite et à l'émigration des perles de la section du cours d'eau où la prédation était intense. En présence de truites dans un aquarium de laboratoire, le comportement d'évitement des prédateurs a amené les perles à préférer le substrat foncé sur lequel elles étaient moins visibles pour les truites. Les perles consommaient beaucoup moins de proies (vers blancs enchytréidés) sur une période de 24 h en présence de truites arc-en-ciel de petite taille (2,0–4,0 cm) et de grande taille (10,0–12,0 cm) que lorsqu'il n'y avait pas de truites dans l'aquarium. Le rythme d'alimentation et le choix du substrat ne différaient pas entre les nymphes bien nourries et les nymphes affamées (5 d).

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Much controversy exists concerning whether predaceous fishes significantly influence prey population dynamics in streams. Some field studies on streams indicate no causal relationship between the presence of predaceous fishes and changes in macroinvertebrate density or behaviour (Allan 1982; Reice and Edwards 1986; Culp 1986), while others suggest the opposite (Bowlby and Roff 1986; Schofield et al. 1988). This is in contrast to numerous studies on pond and lake species which have shown unequivocally that fish induce changes in macroinvertebrate use of space (Charnov et al. 1976; Dixon and Baker 1988), activity pattern (Stein and Magnuson 1976; Heads 1985), feeding rate (Dixon and Baker 1988), and density (Henrikson and Oscarson 1978; Flecker 1984; Hershey 1985).

To try to resolve the controversy as to whether predators significantly affect prey population dynamics in streams, we experimented with rainbow trout, *Oncorhynchus mykiss* and the stonefly nymph *Paragnetina media* (Walker), as a model predator–prey system in a southern Ontario stream and in the laboratory. This predator–prey combination was chosen because rainbow trout densities in southern Ontario streams are typically high (i.e. 20.0–35.0 $g \cdot m^{-2}$; Wainio et al. 1972), and because several studies have shown that *P. media* alter their behaviour in the presence of rainbow trout, thus suggesting that stoneflies may perceive trout as a threat (Feltmate et al. 1986; Williams 1986; Feltmate and Williams 1989).

The objectives of this study were to determine whether rainbow trout reduce the population density of *P. media* in the field, and if so, to quantify how much of this is due to emigration and how much to predation. In the laboratory, we examined whether predator avoidance behaviour would influence changes in substrate selection and feeding rate by both well-fed and starved *P. media*, with trout absent, with small trout present (3.0–5.0 cm), or large trout present (10.0–12.0 cm) in aquaria.

Methods

A fish enclosure–exclosure field experiment was used to determine whether density of *P. media* would change following exposure of nymphs to rainbow trout. The study was done in the Pine River Tributary, Ontario (44°07′N, 79°08′W), between 30 June and 17 August 1988. The tributary was approximately 1.0 m wide by 0.1 m deep. Current speed ranged from 0.0–0.6 $m \cdot s^{-1}$ with a mean flow of 0.32 $m \cdot s^{-1}$. Substrate size ranged from small pebbles (0.5–1.0 cm diameter) to large boulders (>25.0 cm diameter).

This stream was particularly suitable for this study because it contained a large population of *P. media*, and *O. mykiss* was

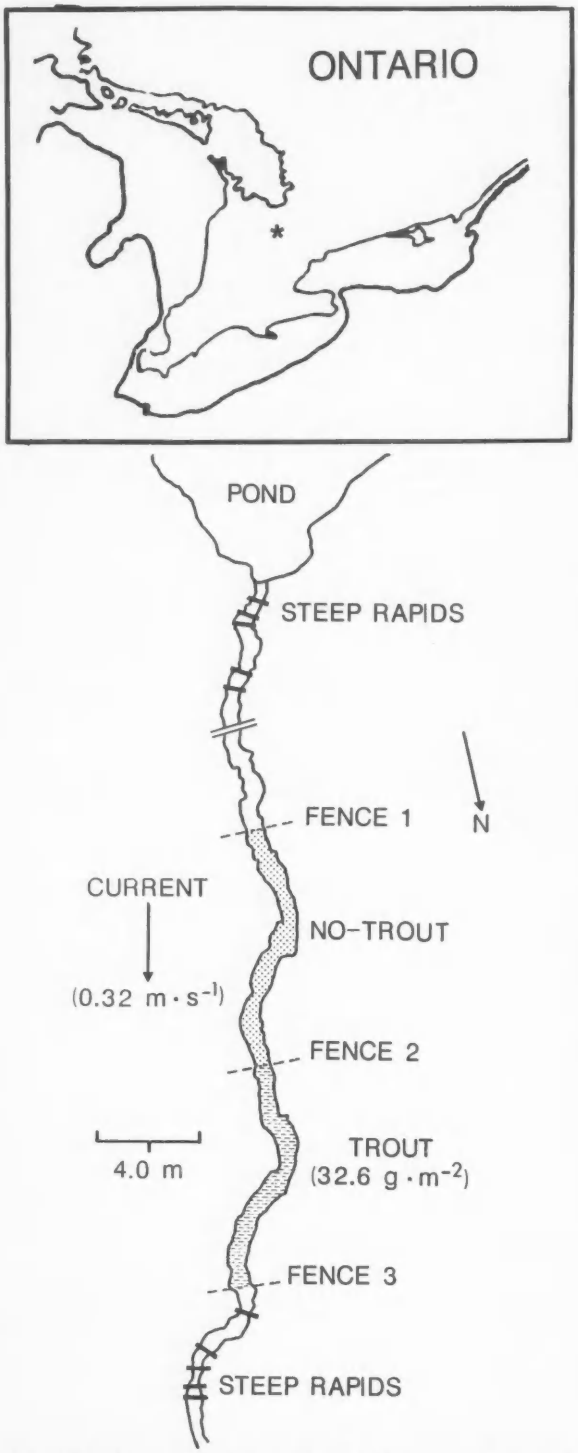

FIG. 1. Pine River Tributary field site, showing trout and no trout experimental sections. The pond was 180 m upstream from fence 1. Asterisk in inset shows location of the tributary on the Niagara peninsula, Ontario.

resident. Two weeks prior to starting the experiment, we seined a section between a downstream rapids and a pond (Fig. 1) to remove existing trout, although only three were found. This low density probably occurred because trout could only circumvent the downstream rapids during the early spring when discharge was high, to be followed later in the season by fish dispersing back downstream.

We prepared two sections in the stream, each 13.0 m long and 13–14 m^2 surface area, using wire fences (1.3-cm mesh) which were 2.4 m in width × 0.8 m high. The two sections were continuous, the upper section with "no fish" and the lower section with "fish." The lower section was used for trout, rather than the upper, to preclude the possibility that fish odours might have affected stonefly behaviour, as has been shown to occur in *P. media* (Williams 1986). The upstream end of the fishless section was also fenced to prevent entry of any fish not caught by seining. About 30–40% of the stream was shaded by 2–3 m high beech (*Fagus grandifolia* Ehrh.), elm (*Ulmus americana* L.), dogwood (*Cornus* spp. L.), watercress (*Nasturtium officinale* Murb.), and spotted jewelweed (*Impatiens capensis* R. Br.).

To determine what proportion of any observed reduction in stonefly density was due to emigration or predation by trout, we estimated the total number of nymphs consumed by trout and subtracted this from the total reduction in numbers of nymphs in the enclosure to give the number emigrating, if any. The number of stoneflies that trout could consume was estimated by calculating, (1) gut clearance time of trout and, (2) the standing crop of stoneflies in trout guts in the enclosure. Gut clearance time was estimated in the laboratory and standing crop was measured in the trout enclosure.

Gut clearance time for trout (10.0–12.0 cm length) was estimated by housing them individually in aquaria in the laboratory and starving them for 2 d; they were held at 18°C, equivalent to that of the Pine River Tributary. After 1 d, none of the fish continued to defecate in the aquaria, thus 2 d was ample time to ensure their guts were empty. After 2 d of starvation, we released two stoneflies into each of the aquaria containing trout, and the nymphs were consumed immediately. From the time prey were ingested, we checked the aquaria every 4 h for trout faeces and we used the time between prey ingestion and defecation to estimate the gut clearance rate of the trout. This procedure was replicated eight times, each time with a different trout.

To estimate the standing crop of stoneflies in trout guts following exposure, trout were released into the lower enclosure and were left undisturbed for 4 d. This relatively short exposure period was used because we wanted to determine the number of nymphs trout could consume from a system that had otherwise experienced little predator stress. Thus, the number of *P. media* in fish guts following a 4-d exposure would be representative of those nymphs most vulnerable to trout. The exclosure, in which no fishes were present, was the control.

To estimate the stonefly density before the release of fish, 15 random Hess samples (0.1 m^2; Hess 1941) were taken, to a depth of 10 cm (solid substrate), in both enclosure and exclosure sections. As each Hess sample was taken, the contents were spread evenly over the bottom of a white-bottomed sorting tray (25 × 25 cm), and they were then systematically searched to determine the number of *P. media* present. In preliminary trials we found that all stoneflies in the trays could be found using this method. After recording the number of stoneflies present per Hess sample, the contents of each tray, including

P. media, were immediately returned to the stream. Stoneflies were placed directly onto substrate, to which they immediately clung.

After determining the density of stoneflies in both sections of the stream, the entire system was left undisturbed for 7 d, which we assumed was sufficient time for the stoneflies to recover from any effects of sampling. After the recovery period, seven wild rainbow trout (10.0–12.0 cm in length, total biomass 25.6 $g \cdot m^{-2}$) were released in the enclosure. These trout were caught by angling with barbless hooks in a downstream section of the Pine River, and they were released in the enclosure on the day of their capture. The trout were left undisturbed in the enclosure for 4 d. The enclosure and exclosure sections were then resampled to determine stonefly density. After collecting stonefly data, all trout were recaptured using a hand-held fishing net, to determine the mean number of stoneflies per trout stomach.

This experiment was replicated three times, with an 8-d recovery after each trial, followed by a 7-d premanipulation estimate of stonefly density. Water temperatures during the replicate trials were approximately 18°C. Since rainbow trout are crepuscular feeders (Bisson 1978), we replicated trials to determine the mean daily standing crop of stonefly nymphs/trout gut by capturing fish at 10:00 in two of the trials and at 21:00 in the other. The standing crop of stonefly nymphs/trout gut was averaged for all trout caught during morning and evening.

In the laboratory, we examined the influence of trout on stonefly escape responses and feeding behaviour. Stoneflies used in this experiment were individuals in their second year of growth (head capsule width >3.0 mm, Harper 1973). Larger nymphs were used because trout typically feed more on larger prey (Ware 1972; O'Brien et al. 1976; Werner et al. 1983; Allan 1984).

Paragnetina media were collected from Duffin Creek, Ontario (44°49′N, 79°08′W). In the laboratory, nymphs were housed individually in large aerated containers and were fed enchytraeid whiteworms ad libitum. Previous experiments have shown that *P. media* will consume, and subsequently moult, when fed on this diet (Feltmate et al. 1986).

We tested whether *P. media* prey consumption and behaviour would change under conditions of trout absent, small trout present, or large trout present. Replicates of this experiment were run in opaque plastic aquaria (18 cm wide × 28 cm long × 13 cm deep) that were filled with dechlorinated water and maintained at 18°C in an environmentally-controlled room. The bottom of each aquarium was roughened with sandpaper to enable the nymphs to crawl. An aerator circulated and oxygenated the water. A dark brown cube-shaped substrate (5 × 5 × 5 cm), constructed from commercial tiles and held together from the inside with silicone glue, was placed at one end in each aquarium. Previous experiments have shown that *P. media* choose dark substrate over light, and that nymphs on dark substrate are less vulnerable to predation by rainbow trout (Feltmate and Williams 1989). Thus the dark substrate represented a relatively safe refuge for the stoneflies. A plastic food cup (2.0 cm diameter × 1.5 cm high) was placed at the end of each aquarium opposite the cube. Within each food cup we placed three enchytraeid whiteworms of uniform length (1.5–2.0 cm). Each cup was covered with nylon screen (mesh diameter 0.8 cm) that allowed stoneflies, but not trout, to enter cups and consume whiteworms. At the beginning of each trial (11:00) one stonefly was released per aquarium. Only one stonefly was used, to preclude the possibility that intraspecific interference might influence the behaviour of nymphs. Upon release, a nymph would normally crawl onto the dark substrate within 2–3 min. In trials requiring the presence of a predator, one trout was released per aquarium 0.5 h after the release of the stonefly. The small trout would periodically bite the stoneflies but they could not consume them. To prevent large trout (10.0–12.0 cm) from consuming nymphs, we used hatchery-reared trout that did not feed for approximately 1 wk after arriving in the laboratory. We therefore ran trials with large trout within this 1-wk period. To ensure that after 24 h all whiteworms could be located in food cups, we also ran six replicates each of tests with no trout, or with small or large trout and no stoneflies.

Twenty-four hours after the release of *P. media*, under conditions of no trout, or small or large trout present, we recorded the number of whiteworms consumed, and whether nymphs rested on the dark cubes, or on the inside of the food cups, on the outside of the food cups, or on the aquarium bottom. Twenty-four replicates of each predator condition were performed. To determine whether starved nymphs responded differently to predators as compared with well-fed nymphs, the experiment was repeated exactly as described above, but with stoneflies that had been starved for 5 d prior to their release in aquaria. We know of no data pertaining to whether stoneflies in streams are food limited or not. Thus, by using both well-fed and starved nymphs in these experiments, we encompassed a range of potential responses *P. media* could have, as dictated by hunger level, to conditions of no trout, or small or large trout present.

Results

The mean (± 1SE) daily standing crop of stoneflies per trout gut was 0.17 ± 0.041. A Kruskal–Wallis test indicated no difference ($P>0.05$) in the number of stoneflies/stomach for individuals caught at 10:00 and 21:00.

We observed no faeces in aquaria 4 h and 8 h after trout were fed. However, after 12 h numerous stonefly body parts were found in all eight aquaria. A siphon was used, at the 12 h check, to remove faeces from all aquaria. At the 16 h check almost no stonefly body parts were found. Therefore, for trout held at 18°C, we estimated the gut evacuation time to be approximately 10 h (half-way between the eight and 12 h check).

Stonefly density data, for all samples, were normally distributed (Kolmogorov–Smirnov Goodness of Fit, $P>0.05$ in all cases), and all variances were homoscedastic (F-max, $P>0.05$ in all cases). The three replicate field experiments were, due to physical limitations, temporally pseudoreplicated (Hurlbert 1984). Therefore, we used paired t-tests to compare the stonefly density data collected, within enclosure and exclosure sections, during the first, second, and third replicates. Four day exposure periods showed a significant reduction between initial and final stonefly density in the trout enclosure (paired t-test, $P<0.05$, Fig. 2), and a slight, yet nonsignificant change in density in the exclosure during the same period ($P>0.05$). Background changes in stonefly density in the enclosure, not related to the presence of trout, were determined based on the marginal reduction in density observed in the exclosure section. The percent of the reduction in stonefly density attributable to the direct effects of trout predation versus nymphal emigration was 41.2 and 58.8%, respectively, which was not significantly different from a ratio of 2:3 (Chi-square, $P>0.05$).

In the laboratory experiments, 92% (132/144) of all observations found stoneflies on dark cubes or within food cups, thus

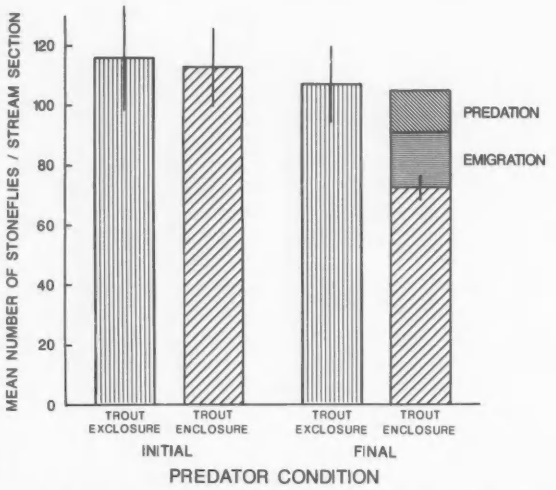

FIG. 2. Mean number of stoneflies, over three replicates, in the trout enclosure and exclosure prior to the introduction of trout into enclosures (initial), and 4 d later (final). Predation and emigration indicate the reduction in the stonefly population per stream section attributable to each process. Samples from each replicate were averaged to give the overall mean (± 1SE).

only data for the distribution of nymphs on cubes or within cups are presented. Stoneflies on cubes always occurred on the sides of the cubes rather than on the top surface, and stoneflies at food cups were almost always observed within the cups rather than on the outside.

A two (well-fed or starved nymphs) by three (no trout, small trout, or large trout) contingency table analysis indicated that the number of *P. media* found on dark cubes across the six conditions was uneven ($P<0.05$, Fig. 3a). Chi-square analysis showed no difference between the number of starved or well-fed nymphs observed on dark cubes ($P>0.10$), however the presence of trout did influence substrate selection ($P<0.05$). Few stoneflies selected dark cubes in the absence of trout, more nymphs occurred on cubes when small trout were present, and a relatively high number selected dark cubes in the presence of large trout.

Contingency table analysis (two by three) also indicated that the number of stoneflies found within food cups, across all six conditions, was uneven ($P<0.05$, Fig. 3b). Chi-square analysis indicated that the number of stoneflies found within food cups did not differ between well-fed or starved nymphs ($P>0.10$), but trout produced an effect ($P<0.05$). Stoneflies were found in high densities within food cups in the absence of trout, relatively few nymphs occurred in cups in the presence of large trout, and an intermediate number selected cups when small trout were present.

Without stoneflies, all whiteworms were recovered from food cups in 18 aquaria after 24 h regardless of predator condition. Thus, any disappearance of whiteworms from aquaria in which *P. media* were present was attributable to the stoneflies.

The number of whiteworms consumed by both fed and starved stoneflies, regardless of trout presence, was normally distributed (Kolmogorov–Smirnov Goodness of Fit, $P>0.05$ in all cases), and variance between conditions was homoscedastic (F-max, $P>0.05$ in all cases). Two-way analysis of variance (ANOVA) indicated an effect of fish ($P=0.0001$), but no

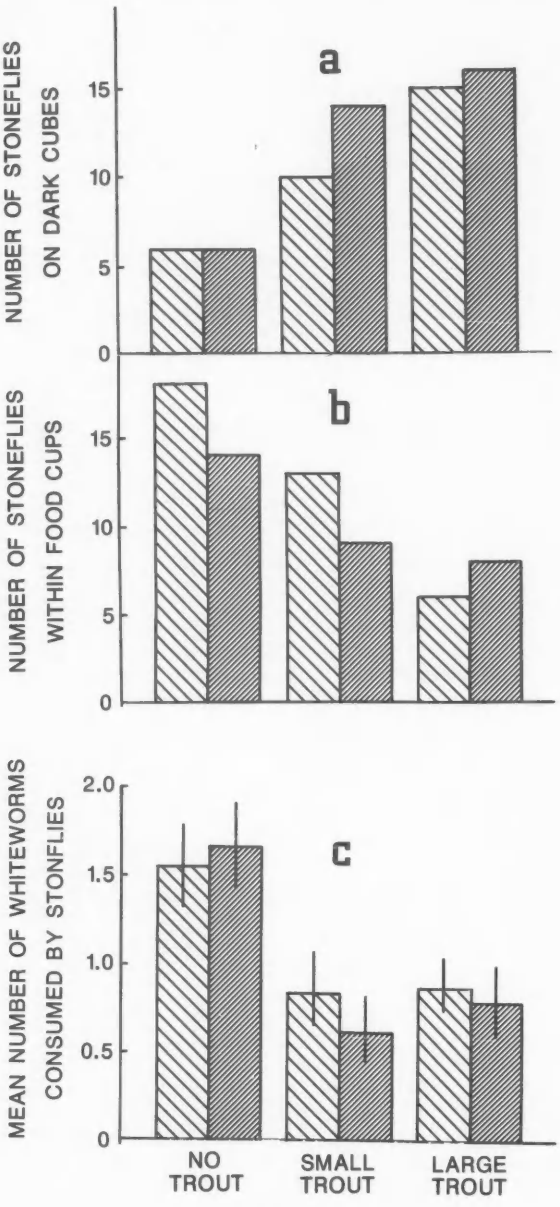

FIG. 3. (a) Number of nymphs observed on dark substrate, (b) number of nymphs observed within food cups, and (c) mean stonefly prey consumption (± 1SE), under conditions of no trout, small trout (3–5 cm), or large trout (10–12 cm) present in aquaria. Light hatching indicates response of stoneflies starved for 5 d prior to their use in experiments, while dark hatching indicates response of well-fed nymphs. Each of the six combinations of predator and nymphal feeding condition was replicated 24 times. Data for (a) and (b) were based on counts of stoneflies (one per aquarium) on dark substrate or within food cups, respectively.

effect of hunger level ($P>0.75$), nor an interaction between fish and hunger level ($P>0.70$), on the number of prey consumed by *P. media* (Fig. 3c). Twice as many whiteworms were consumed by stoneflies, both fed and starved, without trout than with small or large trout present.

Discussion

A fish predator, rainbow trout, reduced the density of a large stream invertebrate, the stonefly nymph *P. media*. Two mechanisms contributed approximately two-fifths and three-fifths, respectively to reducing the population density of stonefly nymphs by 35% in the presence of salmonids; (1) direct consumption of *P. media* by trout, and (2) apparent emigration by *P. media* from the section of stream where trout were present. Our results do not corroborate the findings of Allan (1982); Reice and Edwards (1986); and Culp (1986), all of whom suggest there is no evidence that fish have a significant influence on invertebrate population density. This discrepancy may have arisen because previous experiments used relatively low levels of predator stress. The Colorado stream in which Allan (1982) performed his experiment was initially infertile (trout biomass 4.86 $g \cdot m^{-2}$) and, following a subsequent 75% reduction in trout biomass in a 1220 m section of stream, Allan observed no significant decreases in density or drift of macroinvertebrates between experimental and upstream and downstream control sections. However, because the stream was initially infertile, the probability of finding differences in density or drift between natural and manipulated sections was minimal. Using enclosure–exclosure experiments, both Reice and Edwards (1986) and Culp (1986) found no significant differences in insect assemblages between cages with and without salmonids. However, the fish used as "predators" in the cages were fry of approximately 2.0 g wet weight. Fry this size can feed only on very small insects and, as Reice and Edwards (1986) suggest, "trout fry are just not very efficient predators." In our study, we used a high, but natural, salmonid density (25.6 $g \cdot m^{-2}$, typical of southern Ontario streams, Wainio et al. 1972), and the rainbow trout released in enclosures were relatively large (approximately 30.0–50.0 g wet weight or 10.0–12.0 cm in length). Our results support the findings of Schofield et al. (1988), that brown trout (*S. trutta*) reduced the density of the caddisfly *P. conspersa* in small stream enclosures, and of Bowlby and Roff (1986) where, in a survey of streams in southern Ontario, they found predation to have more of an influence on the invertebrate assemblage than food supply.

The large proportion of the *P. media* population that apparently emigrated from the predator enclosure indicated that the stoneflies may have perceived the rainbow trout as a threat, thus they emigrated in an attempt to escape. Several laboratory studies have shown that *P. media* respond behaviourally to *O. mykiss*. Williams (1986) showed that *P. media* increased their frequency of movement in recirculating tanks in the presence of rainbow trout, and Feltmate et al. (1986) showed that *P. media* altered substrate selection towards larger substrate on which they were less vulnerable to predators. Feltmate and Williams (1989) have shown, both in the laboratory and field, that given a choice between light and dark substrates, *P. media* choose dark substrate on which they are less vulnerable to predation by rainbow trout. In laboratory studies, Soluk and Collins (1988) found that the perlid stonefly *Agnetina capitata* (Pictet) changes its position and frequency of movement on bricks in the presence of the mottled sculpin, *Cottus bairdi* (Girard). These laboratory experiments suggest that one might expect *P. media* to emigrate from a section of stream with a high predator density.

A reduction in the number of prey consumed by *P. media* in aquaria with trout present could potentially reduce stonefly growth and development. As defined by Butler (1984), growth refers to an increase in organism size, whereas development is the physiological and morphological progression toward reproductive maturity. Stoneflies would inevitably grow more slowly as they fed less in the presence of trout. The body weight of *P. media* increases substantially prior to emergence (Heiman and Knight 1970), and this increase is probably related to reproduction as maturation of ovarioles occurs during the final instar in this species (Harper 1973). Since adult *P. media* cannot feed (Hynes 1976), the total energy that they channel into reproductive efforts must be obtained during the aquatic stage. Therefore, predator-induced stress on stoneflies, resulting in the observed reduction in nymphal feeding, would likely result in decreased development of *P. media*.

Our experiments indicate that rainbow trout can influence stonefly density, feeding behaviour, and distribution. What is now needed in stream ecology are field experiments in which the effects of fish predators on prey population dynamics can be examined over several seasons. Krebs (1988) has commented that, "There have been relatively few attempts to manipulate predators . . . to test hypotheses about the role of predation in population dynamics." Although Krebs made this comment in reference to field studies on mammals, it applies equally to studies on predaceous fishes and their role in affecting invertebrate populations in streams.

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Relationship of Condition of Walleye (*Stizostedion vitreum*) and Northern Pike (*Esox lucius*) to Water Clarity, with Special Reference to Dauphin Lake, Manitoba

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Craig, J. F., and J. A. Babaluk. 1989. Relationship of condition of walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*) to water clarity, with special reference to Dauphin Lake, Manitoba. 46: 1581–1586.

An examination of 37 lakes in the central region of Canada revealed that the summer condition of northern pike, *Esox lucius*, was correlated with Secchi depth but there was no such correlation for walleye, *Stizostedion vitreum*. A study of the diets of the two predatory fish coexisting in a prairie lake, showed overlap in the food items selected in July. Food density did not appear to be limited. Walleye food consumption rose from about 1% bodyweight in the spring to 2% in late summer and was less than 1% in the late autumn and early winter. Pike food consumption was similar except it rose to over 3% in the early winter when the lake froze over and the water cleared. High turbidity in the prairie lake during the open water period may have reduced the ability of pike to feed.

L'examen de 37 lacs du centre du Canada a révélé que la condition du grand brochet, *Esox lucius*, en été était en corrélation avec la profondeur de Secchi, mais qu'aucune corrélation de ce type n'existait pour le doré, *Stizostedion vitreum*. Une étude sur les régimes alimentaires des deux poissons prédateurs coexistant dans un lac des Prairies a révélé un chevauchement dans les aliments choisis par les poissons au mois de juillet. La densité des aliments ne semblait pas limitée. La consommation du doré s'élevait à environ 1 % de son poids corporel au printemps et à 2 % à la fin de l'été et était inférieure à 1 % à la fin de l'automne et au début de l'hiver. La consommation alimentaire du brochet était semblable sauf qu'elle atteignait plus de 3 % au début de l'hiver au moment de l'engel et de la clarification des eaux. La forte turbidité du lac des Prairies pendant la saison d'eau libre pourrait avoir réduit la capacité du brochet à se nourrir.

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The purpose of this paper is to test the hypothesis that differences in condition in northern pike, *Esox lucius* can be explained in part by differences in the turbidity of lakes. The high turbidity of large, shallow prairie lakes during the ice free period may prevent pike from seeing their prey and feeding to satiation while having little or no effect on walleye, *Stizostedion vitreum*.

Over its range the optimum habitat of pike appears to be clear, warm, slow, meandering, heavily vegetated rivers or warm weedy bays of lakes (Scott and Crossman 1973). Flooded terrestrial and wetland vegetation in the spring is important to the embryo and larval stages but the success of spawning will be limited by the carrying capacity of the summer habitat (Inskip 1982). Young-of-the-year pike disperse from the spawning area but pike of all ages continue to frequent shallow areas with vegetation. Young pike are especially dependent on this type of habitat. Pike are primarily diurnal and their style of hunting requires cover, usually aquatic plants or submerged logs. There is evidence that the lateral line may have some importance in the early detection of prey (Disler 1967). Walleye also depend on high water levels at spawning time and high spring run-off is often correlated with a successful year class (Lysack 1986). Unlike the pike, the walleye is an open water shoaling fish and feeds mainly at dusk or at night (Ryder 1977). Like the pike it is a visual predator but is able to function efficiently at low light levels due to the tapetum lucidum in the eye (Ali and Ancti 1977).

Walleye and northern pike coexist in the large, shallow, and turbid lakes of the prairie region of Canada and both are important in the sport and commercial fisheries. Dauphin Lake, Manitoba (51°17′N, 99°48′W) is a typical prairie lake having a surface area of 522 km^2 and maximum and mean depths of 3.5 and 2.1 m, respectively. Pike caught in the summer in the lake by sport fishermen are often noted to be in poor condition (low weight for a given length) and are called 'snakes' by the fishermen. Walleye from the same lake are in excellent condition. Abundance of these species must be a major factor in determining condition but poor condition of pike is also probably due to the limitation of optimum habitat for pike.

Methods

An initial investigation was made to test the theory that increased turbidity has a negative effect on pike condition but not on walleye condition. A survey of the literature provided data on 37 walleye–pike lakes mainly from Manitoba. Fork length (L) and weight (W) were used to estimate the weights of standard 350 mm walleye and 500 mm pike during the period of July and August. These estimates were based on length and weight relationships derived by the least squares regression:

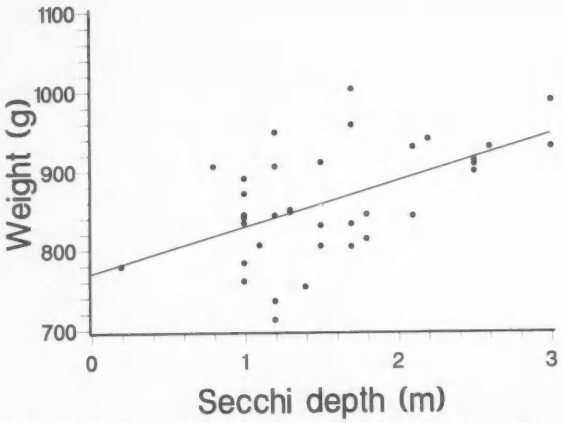

FIG. 1. Weights (grams) of a 'standard length' 500-mm northern pike and Secchi depth (metres) from 37 lakes sampled in July and August. (Data derived from Craig and Smiley 1986; Derksen and Gillies 1979; Gaboury 1984; Hagenson 1983a,b, 1984, 1986; Hagenson and O'Connor 1979, 1980, 1981; and authors' unpubl. data).

$$(1) \quad \log W = \log a + b \log L$$

where a and b are constants. Turbidity measurements of the lakes were not recorded, so weights of the fish were related to Secchi depth which is a good indicator of water clarity.

A detailed study was made on walleye and pike feeding, growth and condition in Dauphin Lake which has a very low Secchi depth of about 0.25 m in July. Fish in Dauphin Lake were sampled from 1984 to 1987 in the spring (May–June), summer (July–August), and fall (September–October) by 15 gill nets per season set at random in the lake for 12-h periods. Each sampling season lasted for approximately 2 wk. The lake was divided into 38 squares of about the same area and gill net sites were selected from random number tables at the beginning of the year. Each gill net was 120 m long and 1.8 m deep and was made up of six equal length panels of 38, 64, 89, 102, 108, and 140 mm of stretched mesh. Further samples of fish were collected in winter (November–December) from commercial fishermen who fished under the ice, mainly for walleye, using 108-mm mesh nets. Samples of fish were also collected during different seasons from 1982 to 1984 by gill netting but not by the above standard techniques. All fish caught were measured (L, millimetres) and weighed (grams). Sex and maturity stage were recorded and ageing structures were taken (opercula for walleye and cleithra for pike).

Length and weight relationships were calculated (equation (1)). Regressions were calculated for each sex, state of maturity, season, and year (1982 to 1987). Differences between regressions were tested by analysis of covariance. Where no significant differences were found, data were pooled.

Diet and food consumption were estimated from July 1985 and 1986 samples captured at 3-h intervals through a 30-h period in the inshore area. Three types of fishing gear were used, a standard gill net, a pound net ($3.1 \times 3.1 \times 2.0$ m, 25.4-mm stretched mesh) and a 5.7-m otter trawl, which also captured small, forage fish. An effort was made to obtain at least 10 fish of each species of the widest possible size range for each time interval. Captured fish were treated in the same way as those captured by seasonal gill netting except the stomachs were carefully dissected out and placed in 5% formaldehyde to arrest digestion. On returning to the laboratory, the stomachs were deep frozen until they were examined. The amount of food in the stomach was first subjectively estimated by a points system from 0 = empty to 4 = full (Craig 1978). The contents of the stomach were then identified and enumerated. Dry weight was estimated for each prey species after heating in an oven at 85°C to a constant weight.

Prey fish caught by otter trawl were sorted into species, counted and the total for each species weighed. Geometric mean numbers per haul were calculated from the transformation $\ln(x+1)$ to allow for zero counts and because the variances in the catches were found to be larger than the mean catches. Numbers of animals per cubic metre were estimated after calculating the volume swept by the trawl. This was based on trawling speed, trawl time, and area of trawl mouth.

TABLE 1. Values of the intercept a (equation (1)) and sample size (n) for mature male and female northern pike and walleye by season from Dauphin Lake, Manitoba. No data available for immature pike in the winter. The coefficient b was 2.8736 throughout for pike, 3.2140 for immatures and mature male walleye, and 2.8780 for mature female walleye.

	Pike		Walleye	
	log a	n	log a	n
Immature males			Immature males and females	
Spring	−4.8367	48	−5.4784	375
Summer	−4.8382	178	−5.4918	687
Fall	−4.8608	30	−5.4642	260
Winter	—	—	−5.4453	324
Immature females				
Spring	−4.8660	54		
Summer	−4.8527	197		
Fall	−4.8551	69		
Winter	—	—		
Mature males				
Spring (spent)	−4.8464	182	−5.4879	63
Summer	−4.8173	293	−5.4803	163
Fall	−4.8247	302	−5.4557	187
Winter	−4.7874	78	−5.4393	480
Mature females				
Spring (spent)	−4.8646	358	−4.5896	37
Summer	−4.8296	230	−4.5715	141
Fall	−4.8400	373	−4.5529	70
Winter	−4.7806	481	−4.5275	194

Results

There was a significant ($P<0.01$) relationship (Fig. 1) between weights (W) of a standard 500-mm pike and Secchi depth in the 37 walleye–pike lakes examined where $W = 786.432 + 46.382$ Secchi depth ($r^2 = 0.21$). No significant ($P>0.05$) relationship was determined for walleye.

Dauphin Lake

Growth and condition

The change in condition of pike and walleye based on the weights of 'standard length' fish derived from regression equations (Table 1) were dissimilar (Fig. 2). The standard lengths of 500 mm for pike and 350 mm for walleye were close to the average size for each species caught. The pike after an increase

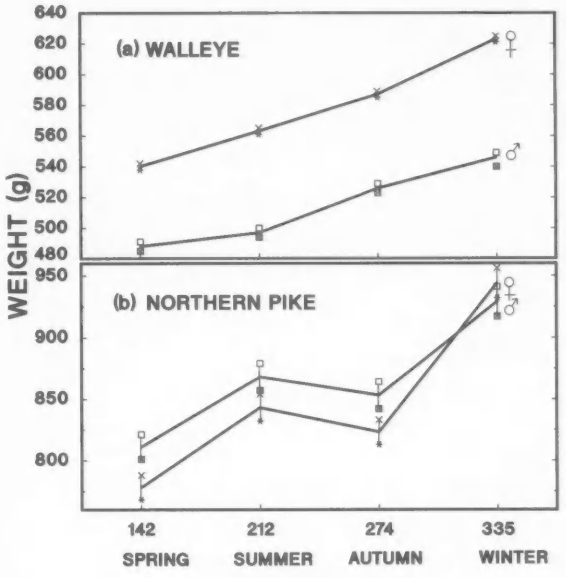

FIG. 2. Seasonal weights (grams) of mature male and female Dauphin Lake (a) walleye and (b) northern pike of 350 and 500 mm length, respectively based on length–weight regressions (Table 1).

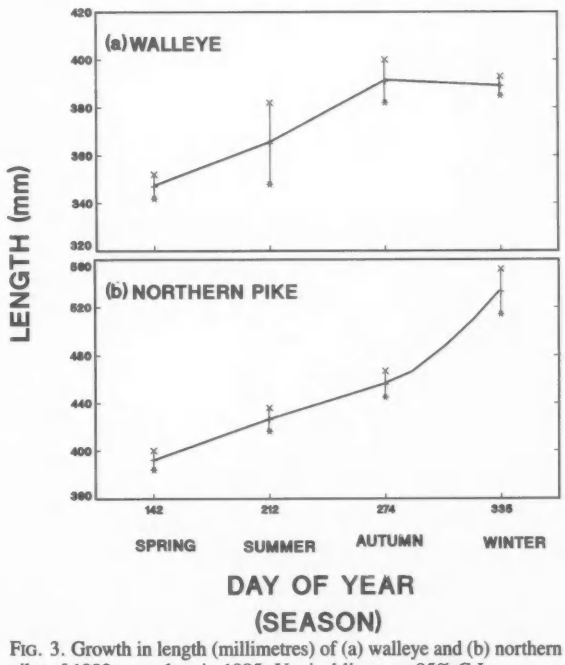

FIG. 3. Growth in length (millimetres) of (a) walleye and (b) northern pike of 1982 year class in 1985. Vertical lines are 95% C.L.

in weight from spring to summer, showed no significant increase from summer to autumn but a rapid increase from autumn to winter. Except in the winter, male pike of the same length as the females were significantly heavier. Evidence that these were real increases in growth rather than differences in weight caused by varying food volume in the stomach is provided by considering single year classes of walleye and pike that were dominant in the lake at the time of the feeding studies, the 1982 year classes at age 3 yr. There were no significant differences ($P>0.05$) in length between sexes at this age and data were pooled (Fig. 3).

TABLE 2. Percentage occurrence of prey species in the stomachs of northern pike and walleye caught in Dauphin Lake in July.

Prey	Northern pike	Walleye
Empty	27.7	26.2
Notropis atherinoides	22.3	41.9
N. cornutus	2.1	1.6
N. hudsonius	4.2	0.0
Percopsis omiscomaycus	28.7	1.0
Coregonus artedii	1.1	2.6
Perca flavescens	10.6	20.9
Stizostedion vitreum	0.0	0.5
Percina caprodes	1.1	0.0
Etheostoma exile	1.1	0.0
Esox lucius	0.0	1.1
Catostomus commersoni	0.0	1.1
Moxostoma macrolepidotum	1.1	0.0
Fish remains	12.8	40.3
Hexagenia limbata	0.0	8.4
Tricoptera	0.0	0.5
Diptera	0.0	0.5
Clam	1.1	0.0
Orconectes virilus	12.8	0.0
Insect remains	1.1	0.0

Food and feeding

Walleye and pike fed on similar food items during July (Table 2). The main differences were that trout–perch, *Percopsis omiscomaycus*, and crayfish, *Orconectes virilus*, were almost exclusively eaten by pike, and the mayfly, *Hexagenia limbata*, were exclusively eaten by walleye. Dietary overlap (Y%) was calculated from:

$$(2)\quad Y = 100\left[1 - 1/2\sum_i (p_{pi} - p_{wi})\right]$$

where p_{pi} and p_{wi} are the frequencies of each prey item i occurring in pike and walleye, respectively (Schoener 1970), and equalled 90.4%. Emerald shiner, *Notropis atherinoides*, and yellow perch, *Perca flavescens*, were particularly important to both predators.

Trout–perch and emerald shiner were the most abundant species in the inshore areas as indicated by otter trawl catches. This was supported by afternoon beach seining in the same area (Table 3; P. Schaap, unpubl. data). Crayfish were not counted in the seine samples. Secchi depth during this period was low, sometimes <0.1 m.

Food consumption

Weights of total dry stomach content were plotted against the wet weight of fish for different periods. Variability between individual fish was high. Regression equations calculated for both arithmetic and log scales relating weight of food and weight of fish were only significant in some cases. Equations based on data broken up into separate taxonomic groups or different sexes or from different fishing gears showed no improvement. No definite trends in stomach fullness of walleye were apparent

TABLE 3. Mean numbers (with 95% C.L.), mean weight, and percentage of catch by number of the major prey species eaten by walleye and northern pike caught by otter trawl in Dauphin Lake, Manitoba. Also given are the percentages by number of each species in seine catches.

Species	Mean number·m^{-3}	(95% C.L.)	Mean weight (g)	Percentage of catch by number otter trawl (%)	Seine (number of fish = 1753) (%)
Trout–perch	0.0066	(0.0045–0.0095)	4.2	52.4	53.5
Emerald shiner	0.0052	(0.0030–0.0085)	1.9	41.3	39.9
Yellow perch	0.0005	(0.0004–0.0008)	10.4	4.0	0.4
Crayfish	0.0002	(0.0001–0.0004)	11.2	1.6	—
Spottail shiner	0.0001	(0.0001–0.0001)	5.7	0.8	6.2

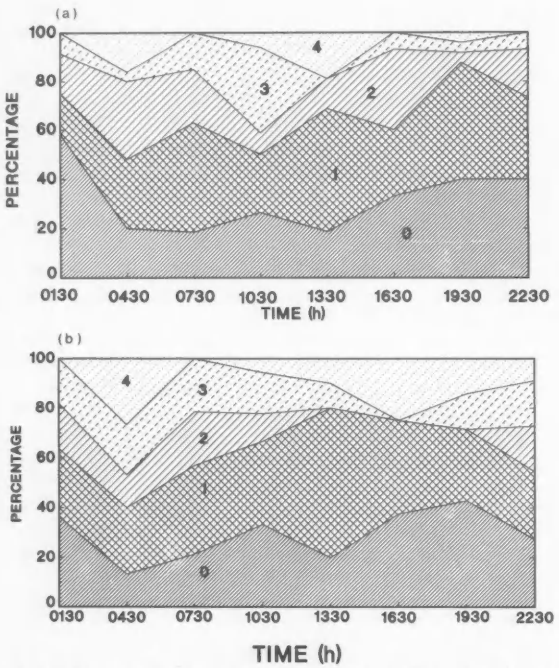

FIG. 4. Percentage of the catch of walleye (a) and northern pike (b) having stomach fullness coefficients 4 to 0 (see method) plotted for each time period.

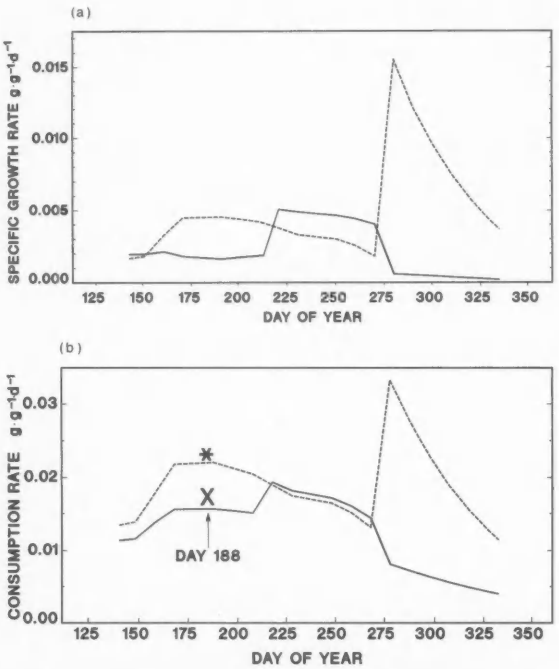

FIG. 5. Specific growth rates (a) and food consumption (b) (gram per gram per day) plotted through the year for walleye (solid line) and northern pike (dashed line) based on a bioenergetics model of 1982 year class in 1985. Also shown on the figure are estimates of food consumption derived from field data on Day 188.

although they appeared to be fullest in the early morning (Fig. 4a). During the early morning and late afternoon, pike stomachs were fullest (Fig. 4b). The total dry weight of fish stomach contents was plotted against total wet weight of the fish for each stomach fullness coefficient. Regression equations were calculated for each set of points and best fits were on a ln–ln scale. Combining data from the regression equations and Fig. 4, the average weights with 95% CL of the stomach contents of a 500 g walleye and pike were calculated for each 3-h period. There were no significant differences in stomach content weight for each species within time periods. The average stomach content (95% CL) was 0.347 g (0.111 to 1.172) for walleye and 0.969 g (0.271 to 3.880) for pike.

The weight of food consumed per day by walleye was estimated from

$$(3)\quad C = 24\bar{S}K$$

where $\bar{S}$ is the average stomach content in 24 h and K is the rate of gastric evacuation (Craig 1978, 1987). A value of $K = 0.256$ mg·g^{-1}·h^{-1} was used based on a water temperature of 20°C from Swenson and Smith (1973). Assuming a water content of the prey species of 75% (J. F. Craig, unpubl. data), the daily consumption of 500-g walleye was calculated as 0.017 g·g^{-1}·d^{-1}.

Consumption of pike was based on the model of Diana (1979):

$$(4)\quad C = \frac{\bar{M}Z}{BN}$$

where $\bar{M}$ is the weight of food in the stomach (based on a stomach fullness coefficient of 4), Z is the number of pike with food in their stomachs out of a sample size of N and B is evacuation

time. From Diana (1979) $B = 1.25$ d. If it is assumed that 1 g dry weight of prey species contains 5 KCal, $C = 0.023$ $g \cdot g^{-1} \cdot d^{-1}$ for a 500-g pike.

Specific growth rates (Fig. 5a) and food consumption (Fig. 5b) were estimated using the bioenergetics models of Hewett and Johnson (1987) for walleye and pike of the 1982 year classes at age 3 yr based on growth data. These estimates and those derived from the feeding study show some agreement for both walleye and pike. The increase in pike consumption and growth in the early winter coincided with the appearance of ice on the lake. At this time the water cleared and visibility was enhanced. Over 80% of the pike stomachs examined from gill net captures were full and contained mainly cisco, *Coregonus artedii*.

Discussion

Evidence from the examination of walleye–pike lakes suggests that water clarity influences condition and thus the feeding and growth of pike but not walleye. Although only about 21% of the variance in pike weight is explained by Secchi depth, the relationship between the two is significant. The remaining variance is probably explained by environmental factors such as lake depth, latitude (temperature), and total dissolved solids and genetic differences. Many of the lakes considered are in the Precambrian Shield and are less productive than Dauphin Lake. However pike exhibit improved condition the further north they are found (Doyon et al. 1988).

There are few observations on the effects of turbidity on food consumption and growth of walleye and pike. High levels of turbidity are characteristic of large shallow prairie lakes in the summer when strong winds can quickly mix bottom sediments into the water column. Walleye increase their activity and feed in the daytime in lakes of high turbidity (Ryder 1977). Pike become more pelagic and move away from inshore areas when wind action affects the bottom of the littoral area (Chapman and Mackay 1984; Vollestad et al. 1986). Although both predators are visual feeders, other sensory organs are involved in prey detection (Regier et al. 1969). No evidence has been seen by the authors to suggest that turbid waters reduce the consumption of prey and thus the growth of walleye. Vollestad et al. (1986), found that despite higher prey density, pike did not grow so well in a turbid river system as in a less turbid and less productive lake.

Growth of northern pike in Dauphin Lake during the summer is depressed although the water temperature is near an optimum for growth (20°C; Casselman 1978). Growth must be retarded by low food consumption. However, food density does not appear to be limiting. There is considerable overlap in the diet of the walleye and pike but walleye growth is not restricted in summer. P. R. Schaap (unpubl. data) found in Dauphin Lake in July that prey density of emerald shiner exceeded 400 $mg \cdot m^{-3}$, the density required for maximum consumption by walleye (Swenson 1977).

Estimates of food consumption from field studies and growth data show reasonable agreement. Therefore, growth data alone may be sufficient for estimating values for the bioenergetics equation. The data from Dauphin Lake showed that the pattern of food consumption and growth of walleye through the year was fairly typical. Food consumption rose from about 1% body weight in the spring to 2% in the late summer and was less than 1% in the late autumn and early winter. The values for July in Dauphin Lake were lower than those calculated by Swenson and Smith (1973) for walleye in Lake of the Woods for the same month which were 3% body weight. Food consumption of pike in Dauphin Lake was about 1% body weight after spawning, rising to 2% in the summer and falling to 1% in the autumn but rising again to over 3% in the early winter when ice appeared on the lake. At this time the pike were able to take advantage of clear water conditions and the spawning concentrations of cisco. Diana (1979) found that pike food consumption in Lac St. Anne was highest during June and July and then it declined through the late summer and autumn. This is probably the normal sequence in pike populations.

Further experiments will be needed to test the effects of various levels of turbidity on prey capture by pike. The circumstantial evidence at present suggests that turbidity reduces food consumption and thus growth.

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Ecological and Genetic Studies on *Dreissena polymorpha* (Pallas): a New Mollusc in the Great Lakes

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Dreissena polymorpha, a bivalve mollusc endemic to Europe, has established a population in Lakes St. Clair and Erie, likely as a result of ballast water discharge. Allozyme studies showed that the Lake St. Clair population was polymorphic at 73.9% of the loci examined and that individual heterozygosities averaged 31.6%. This high level of genotypic diversity indicated that the population was founded from a substantial number of individuals and did not undergo a bottleneck subsequent to founding. The population is reproducing with peak densities in excess of 200 individuals·m^{-2}. Juvenile settlement occurs in late July and August with veliger larvae preferentially settling on the shells of live mussels. The species appears likely to become a dominant member of the shallow water benthos throughout the lower Great Lakes.

Dreissena polymorpha, mollusque bivalve endémique en Europe, a constitué une population dans les lacs Ste-Claire et Erié, vraisemblablement à la suite de rejet d'eau de ballast. L'analyse des allozymes montre que la population du lac Ste-Claire était polymorphe à 73,9 % des locus examinés et que les hétérozygoties individuelles étaient en moyenne de 31,6 %. Cette grande diversité génotypique indique que la population a été fondée par un nombre important d'individus et n'a pas connu de goulot d'étranglement subséquent à la fondation. La population se reproduit avec des densités maximales dépassant 200 individus · m^{-2}. La fixation des juvéniles se produit à la fin de juillet et en août, et les larves véligères s'installent de préférence sur les coquilles de moules vivantes. L'espèce semble en passe de devenir un membre dominant du benthos des eaux peu profondes dans l'ensemble des Grands Lacs inférieurs.

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The introduction of organisms into the Great Lakes as a result of ballast water discharge has gained importance since the opening of the St. Lawrence Seaway in 1959. Some invading species, such as the mitten crab, *Eriocheir sinensis*, (Nepszy and Leach 1973), and the flounder *Platichthys fleaus* (Emery and Teleki 1978) have failed to establish populations. However, other species such as the cladoceran crustacean, *Bythotrephes cederstroemi* (Berg and Garton 1988; Lehman 1987), and the fish, *Gymnocephalus cernua* have become dominant members of the fauna. The present study reports the establishment of the mollusc *Dreissena polymorpha*, a species likely to become an important component of the shallow water benthos.

Dreissena polymorpha is a member of a small superfamily of bivalve molluscs whose three component genera are restricted to estuarine and freshwater habitats (Morton 1969a). Until the 19th century the species was restricted to the Black, Caspian, and Azov Seas (Stanczykowska 1977), but it has since spread rapidly throughout Europe. For example in 1824 it colonized the London docks and within a century was a dominant component in British freshwater systems (Kerney and Morton 1970). Its rapid population expansion has been linked both to its possession of free swimming veliger larva and to its high fecundity (>30 000 eggs per female). At sites where it has reached high densities, *D. polymorpha* often causes significant economic losses by obstructing flow in the intake channels of hydroelectric installations and water distribution systems (Shtegman 1964: Morton 1969b).

The present study, which shows that *D. polymorpha* has now colonized the Great Lakes, has involved both a preliminary investigation of its abundance and distribution, as well as a survey of genotypic diversity to determine if the population owes its origin to a large number of founders or to a very few. In the latter case, one would expect low levels of allozyme diversity, while high diversity would suggest its origin from a large number of founders.

Materials and Methods

The first individual of *D. polymorpha* (Fig. 1) from Lake St. Clair was collected on June 1, 1988 with a ponar grab. Subsequent collections during June and early July 1988 suggested that the species varied in abundance among sites and stimulated a more quantitative study.

The density of the species was established between August 1–4, 1988 at 10 sites in the lake (Fig. 2). These sites were

FIG. 1. Photograph of *Dreissena polymorpha* (shell length 2.5–2.6 cm).

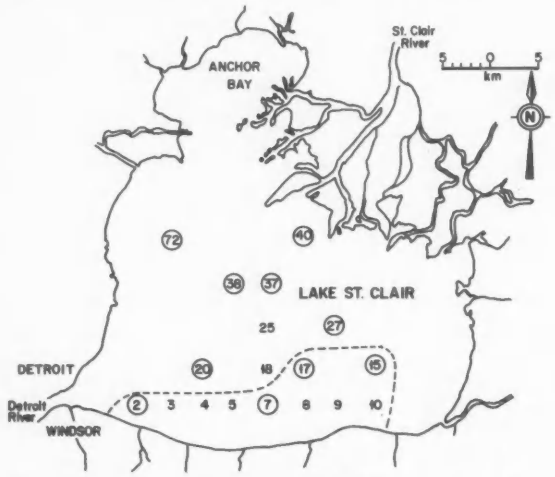

FIG. 2. Map of Lake St. Clair showing sampling sites. Circled numbers indicate sites included in the quadrat analysis, while uncircled numbers refer to transect sites. The dashed line encloses sites where *D. polymorpha* was collected.

chosen from 69 sites on the Lake St. Clair grid (Pugsley et al. 1985) to ensure representation of major sediment types. Sampling intensity was stratified in relation to the abundance of each sediment type within two sites in gravel/coarse sand, four in finer sands, and four in silts. The sites included in each category were chosen randomly from amongst all sites in the lake with an appropriate sediment composition (Pugsley et al. 1988). At each site divers collected all living and dead mussels, as well as all rocks inhabited by *D. polymorpha* from 30 randomly placed 0.2-m^2 quadrats. Collections from 10 quadrats were pooled to produce a sample, so that three samples were obtained from a site, with each containing the animals from 2 m^2 of bottom.

A subsequent survey provided more details of abundance variation around the only site (7) at which large numbers of *Dreissena* were collected in the quadrat study. This survey involved the analysis of *Dreissena* abundances at nine sites along three 10.5-km transects which intersected at site 7. Divers collected a minimum of 15 native mussels at each site and their shells were examined for attached *D. polymorpha*. The dominant mussels at these sites were: *Amblema plicata, Anodonta grandis, Elliptio dilatata, Fusconaia flava, Lampsilis radiata, Lampsilis ventricosa, Leptodea fragilis, Obovaris subrotunda, Pleurobema coccineum*, and *Proptera alata*.

TABLE 1. Substrate type, mean number of mussels and *D. polymorpha*, and proportion of mussels with *D. polymorpha* attached at the quadrat sites. Standard errors are given in parenthesis. Each quadrat is 2 m^2.

Site	Substrate	Mean Mussels per quadrat	Proportion of Mussels with *D. polymorpha*	*D. polymorpha* per quadrat
2	Gravel	11.3(2.0)	0.70(0.1)	96.0(12.3)
7	Gravel	22.6(5.2)	0.90(0.1)	390.0(82.6)
15	Silt	4.0(0.6)	0.23(0.1)	1.0(0.6)
17	Sand	5.0(2.6)	0.45(0.3)	1.7(0.7)
20	Silt	6.3(2.2)	0.0	0.0
27	Sand	5.0(1.5)	0.0	0.0
37	Sand	0.7(0.3)	0.0	0.0
38	Silt	0.7(0.3)	0.0	0.0
40	Sand	0.3(0.3)	0.0	0.0
72	Silt	5.0(2.3)	0.0	0.0

TABLE 2. Proportion of live mussels (*n*) carrying *D. polymorpha*, and mean number of *D. polymorpha* attached to each mussel at 11 Lake St. Clair transect sites.

Site	*n*	Proportion of mussels with *D. polymorpha*	Mean number of *D. polymorpha* per mussel (SE)
2	34	0.70	2.3(0.5)
3	15	0.87	4.3(1.0)
4	15	0.47	1.4(0.6)
5	15	0.60	1.9(0.6)
7	68	0.90	8.2(1.0)
8	12	0.92	17.1(4.7)
9	15	0.73	1.7(0.6)
10	15	0.93	3.9(1.0)
18	15	0.0	0.0
25	15	0.0	0.0
37	2	0.0	0.0

Shell lengths of all *Dreissena* collected in the original survey of 10 sites were determined using a micrometer with a precision of ± 0.1 mm. The ages of 20 individuals in each of two major size classes were determined by shell sectioning. Finally the reproductive status of selected individuals were assessed by examining gonadal tissue at 400×.

Total body extracts were prepared from 64 individuals collected at site 7 and examined for electrophoretic variation at 18 enzymes using cellulose acetate electrophoresis (Hebert and Beaton 1989). Allozyme phenotypes were determined for phosphoglucoseisomerase (*Pgi*) phosphoglucomutase (*Pgm*), mannose-6 phosphate isomerase (*Mpi*), isocitrate dehydrogenase (*Idh*), aldehyde oxidase (*Ao*), lactate dehydrogenase (*Ldh*), fumarase (*Fum*), malate dehydrogenase (*Mdh*), malic enzyme (*Me*), arginine phosphofructokinase (*Apk*), triose phosphate isomerase (*Tpi*), glutamate oxaloacetate transaminase (*Got*), leucyl-alanine peptidase (*Pep*), glycerol-3-phosphate dehydrogenase (*Gpdh*), leucine aminopeptidase (*Lap*), glyceraldehyde-3-phosphate dehydrogenase (*G3pdh*), and esterase (*Est*). *Ao* and *Pgm* showed complex phenotypic variation and were excluded from further consideration, but the remaining enzymes resolved clearly and possessed easily interpretable phenotypes.

Representative voucher specimens from site 7 have been deposited in the National Museum of Canada, Ottawa, catalogue number (NMC 92862).

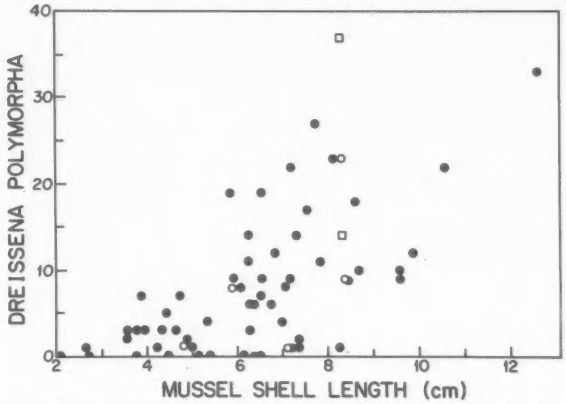

FIG. 3. Relationship between the number of *D. polymorpha* attached to live mussels at site 7 and mussel shell size. Open circles and squares indicate mussels carrying one or two adult *Dreissena*, respectively.

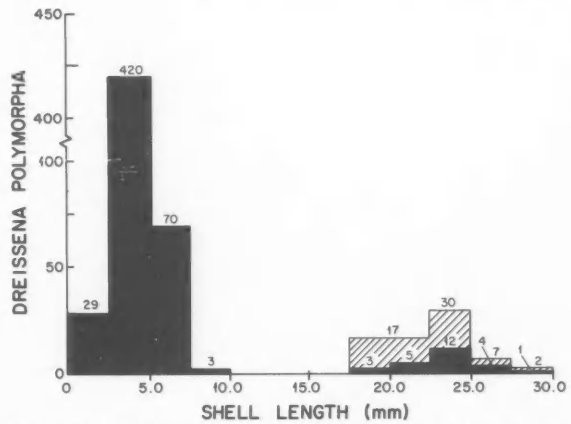

FIG. 4. Length-frequency histogram of *D. polymorpha* from Lake St. Clair in August 1988. Hatched areas represent the supplemental collection of 50 adults.

Results

Distributional Patterns and Demography

The population survey suggested that *D. polymorpha* was restricted to the southeastern portion of Lake St. Clair (Fig. 2) with densities approaching 50 and 200 individuals·m^{-2}, respectively at the two sites (2,7) with gravel substrate (Table 1). At these sites two thirds of the *Dreissena* were attached to rocks and the balance to living or empty mussel shells while in areas with fine substrate (e.g. sites 15,17) all were attached to mussels. The proportion of live mussels carrying *Dreissena* varied from a high of 90% at site 7 to 0% on mussels from the central and northwestern portions of the lake. The transect study (Table 2) confirmed that *Dreissena* was widely distributed in southeastern Lake St. Clair and revealed a site at which individual mussels carried an average of more than 17 *Dreissena*.

At site 7 the number of *Dreissena* attached to individual mussels varied from 0 to 38. There was a significant correlation (Fig. 3) between the number of *D. polymorpha* and mussel shell size ($r^2 = 0.43$, $n = 65$, $p < 0.001$). Mussels with a shell size of 5.5 cm or less never carried more than seven *Dreissena*, (Fig. 3) while large mussels carried up to 38. The location for attachment was clearly nonrandom with *Dreissena* restricted to those portions of the shell which ordinarily protrude above the sediment surface (i.e. excurrent siphon, umbo). Collections at site 7 showed that the shells of dead mussels were less attractive as settlement sites for *Dreissena* than those of live mussels. On average only 25% of these shells carried *Dreissena* (versus 90% of live shells) and the mean number of *Dreissena* per shell was far lower (0.70 ± 0.2 versus 8.2 ± 1.0).

Measurements of shell size at site 7 revealed a bimodal distribution with a complete absence of individuals with shell sizes ranging from 7.7–18.0 mm (Fig. 4). Measurements on a supplemental collection of 50 individuals with shell sizes greater than 80 mm revealed that this gap in the size distribution was real. Individuals larger than 20.0 mm were sexually mature, as evidenced by the presence of spermatoza in their gonadal tissues. Shell sections showed that the largest individuals in the population were 3 yr old. Individuals in the small size class evidently were young-of-the-year as they were absent from collections made in June and early July. Juveniles outnumbered adults in the August collections by a ratio of 20.9:1.

TABLE 3. Allele frequencies and individual heterozygosities (*H*) at 17 polymorphic loci in the Lake St. Clair population of *Dreissena*.

		Allele frequency					
Locus	*n*	1	2	3	4	5	*H*
6-Pgdh	60	.02	.71	.27	—	—	0.22
Est-2	63	.04	.31	.20	.45	—	0.70
Fum	63	.17	.14	.69	—	—	0.49
G3pdh	62	.51	.49	—	—	—	0.44
Got	62	.17	.77	.06	—	—	0.44
Idh	59	.22	.78	—	—	—	0.40
Lap	62	.01	.01	.80	.04	.14	0.24
Ldh	61	.43	.57	—	—	—	0.61
Mdh-1	64	.17	.83	—	—	—	0.16
Mdh-2	61	.78	.22	—	—	—	0.34
Me	51	.46	.54	—	—	—	0.25
Mpi	62	.07	.30	.32	.19	.12	0.69
Pep-1	58	.13	.01	.11	.75	—	0.40
Pep-2	60	.04	.32	.47	.17	—	0.48
Pep-3	58	.29	.71	—	—	—	0.14
Pgi	61	.07	.39	.43	.11	—	0.62
Tpi-1	59	.14	.30	.51	.05	—	0.41

Genetic Diversity

Satisfactory resolution was obtained for 16 enzymes representing 23 loci including *Apk* (two loci), *Est* (three loci), *Gpdh*, *G3pdh*, *Got*, *Fum*, *Idh*, *Lap*, *Ldh*, *Mdh* (two loci) *Me*, *Mpi*, *Pep* (three loci), *Pgi*, *6Pgdh* and *Tpi* (two loci). Seventeen of the 23 loci (73.9%) were polymorphic. Monomorphic loci included *Apk*-1, *Apk*-2, *6Pgdh*, *Tpi*-1, *Est*-1, and *Est*-3. Two pieces of evidence support the view that this phenotypic variation had a genetic basis. Firstly, allozyme phenotypes of putative heterozygotes at the loci were congruent with those expected on the basis of the quaternary structure of the enzyme (Ward 1977). Thus heterozygotes at *Pgi*, *Mdh*, *Got*, *Idh*, *Tpi*-1, and *Me* were triple banded, as expected for dimeric enzymes. Heterozygotes at the monomeric enzymes *Mpi*, *Lap*, *Pep*-1, *Pep*-2, *Est*-2, and *G3pdh* were double banded and those at the tetrameric enzymes *Fum* and *Ldh* were five banded. Secondly, genotypic frequencies at each locus closely approximated

Hardy–Weinberg expectations. Polymorphic loci had an average of 3.1 alleles/locus, while individual heterozygosities, averaged over all 23 loci, were 31.6% (Table 3).

Discussion

Dreissena polymorpha was broadly distributed over southeastern Lake St. Clair with densities varying from 1–200 individuals·m^{-2}. By comparison mean densities of 100–1000 individuals·m^{-2} have been observed in European lakes. The population of *Dreissena* appeared to be growing rapidly, as evidenced by the large juvenile:adult ratio. *Dreissena* has apparently been present in Lake St. Clair for less than 5 yr as an intensive survey of the bivalve mollusc fauna in 1983 failed to reveal its presence (Hebert et al., unpubl. data). Age structure analysis of *Dreissena* from Lake St. Clair indicated that the largest adults in the population were 3 yr of age, suggesting that the initial colonization occurred in 1985.

Studies on European populations (Kornobis 1977; Stanczykowska 1977) have shown that female *Dreissena* first release their eggs when water temperatures exceed 13°C and that egg numbers peak when temperatures rise to 22°C. The eggs are fertilized after release and develop into 70-μm long veliger larvae, which float in the epilimnion for 10–15 d. Once the veligers attain a length of 200 μm they descend to the bottom and transform into postveligers which begin the transition into the adult bivalve morphology. Postveligers are mobile for several days and select an appropriate substrate for settlement and transformation. In European populations the period from egg release to juvenile mussel attachment is at least 3 wk.

In Lake St. Clair the optimal temperature (22°C) for egg release first occurred in late June of 1988, and one would expect, hence, the peak recruitment of juveniles in mid–late July. The initial collections of *Dreissena* from Lake St. Clair in June and early July revealed no juveniles, but they were abundant in the early August collections. Therefore, it seems that reproductive patterns in the Lake St. Clair population resemble those in Europe, but detailed life history studies are needed to verify this.

In Europe individuals of *D. polymorpha* typically begin to reproduce once they reach a shell size of approximately 1 cm after a year of growth. Maximum shell size and age are inversely dependent on temperature with sizes ranging from 3–5 cm and age from 3–6 yr. Survivorship curves are J-shaped with mortality concentated in the presettlement phase. Most populations are dominated by young adults with older age classes less common. The Lake St. Clair population was exceptional as most adults were 2–3 yr old. Indeed, there was an apparent absence of 1-yr old mussels, suggesting that recruitment was poor or absent in 1986 and 1987. It is possible that the abundance of juveniles in the August 1988 samples reflects the first reproduction within the Great Lakes. In view of the long dispersal phase of their veliger larvae, it was surprising that the numbers of juvenile *Dreissena* settling on mussel hosts in Lake St. Clair showed so much micrographic heterogeneity. The failure of *D. polymorpha* to colonize the northern and central portions of the lake is likely attributable to current flow patterns, but it is difficult to understand the factors responsible for nonrandom settlement in the southeastern portions of the lake. The high density of juvenile settlement in areas with the highest numbers of adults suggests that veliger dispersal is curtailed. Long distance dispersal may predominate only in populations which have achieved high densities. One would anticipate that veligers from Lake St. Clair would be exported to Lake Erie, and juveniles were detected in the western and central basins of that lake during late 1988 (J. Leach, Lake Erie Fisheries Research Station, RR2, Wheatley, Ont., pers. comm.).

No genetic data are available on European populations of *Dreissena*, but the current study has shown that the species is exceptionally variable. Individual heterozygosities in the Lake St. Clair population averaged 31.6%, ranking the species in the upper 1 percentile of reported heterozygosity values (Nevo et al. 1984). Its exceptionally high level of genetic variability may account for its success as a colonist. Moreover, the presence of substantial amounts of variation makes it unlikely the Lake St. Clair population of *Dreissena* was either founded from few individuals or went through a severe bottleneck after establishment. The high level of genetic diversity contrasts with the complete lack of allozyme variation in North American populations of another introduced bivalve, *Corbicula fluminea* (Smith et al. 1979). This latter species, however, appears exceptional as most introduced molluscs, especially those with veliger larvae, possess levels of genotypic diversity similar to those in their founder populations (Ward 1989).

There is little doubt that *Dreissena* entered the Great Lakes via ballast water discharge. The likelihood of such an introduction was predicted by an EPS (1981) study which revealed that the ballast tanks of ships entering the Great Lakes contained a diverse assemblage of exotic organisms. Moreover, the numbers of individuals of single taxa were large — in some cases greater than 10^6 individuals per tank. Veliger larvae were numerous in 10% of the ships surveyed, although they were not identified to the specific level.

Ecological information on European populations of *Dreissena* is sufficiently detailed to provide a good basis for predicting the impact of its introduction on North American freshwater habitats. Firstly, as the minimum temperature (16°C) for its successful reproduction is exceeded in all of the Great Lakes except Lake Superior (Pinsak 1976), the species seems likely to colonize all of the lower Great Lakes. Indeed it should, in time, be able to colonize freshwater habitats throughout much of temperate North America. In these habitats it will be most common in the littoral and sublittoral zones, with peak densities of 2000 individuals·m^{-2}. Densities on breakwalls and intake pipes may, however, rise in excess of 100 000 individuals·m^{-2} (Wilhelmini 1922; Clarke 1952). Aside from the economic impacts resulting from the fouling of water intakes, *D. polymorpha* may prove to be an interference competitor of native mussels, especially as it preferentially settles on their shells (Lewandowski 1976). Comparable displacements of the native gastropod fauna have been observed in those sections of the Great Lakes colonized by the introduced gastropods *Bithyinia tentaculata* and *Cipangopaludina chinensis* (Cook and Johnson 1974). Aside from such direct impacts, *Dreissena* has the potential to induce more profound ecological changes — in many European lakes it has been responsible for the development of a unique shell zone. Most European habitats were colonized nearly a century ago and the impact of its arrival on the native fauna was unstudied. By contrast, discovery of the species so soon after its arrival in North America makes possible assessment of both the rate and impact of its spread.

Acknowledgements

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Uptake and Elimination of Coliform Bacteria by Four Marine Bivalve Mollusks

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Bivalve filter feeding mollusks remove suspended bacteria from the ambient water and either sediment them with the pseudofaeces, or ingest and digest them. On the basis of bacterial contamination of water and known pumping rate, accumulations usually exceed expected levels by an order of magnitude. This does not reflect high uptake efficiency of the bivalve, but is a function of the digestive process separating bacterial clusters, thereby increasing inoculative loci both for multiple tube estimates and plate counts. Uptake rates are species specific and temperature dependent and show little correlation with the ambient bacterial loading. Elimination is also species specific and variable.

Les mollusques bivalves filtreurs absorvent les bactéries en suspension dans l'eau ambiante et les décantent avec leurs pseudofèces ou les ingèrent et les digèrent. En se basant sur la contamination bactérienne de l'eau et sur la vitesse de pompage connue, les accumulations habituelles ont dépassé les teneurs prévues d'un ordre de grandeur. Cela ne reflète pas l'efficacité d'absorption élevée des bivalves, mais est fonction du processus de digestion, qui sépare les grappes de bactéries et, par là, augmente les points susceptibles d'inoculation tant dans les estimations à tubes multiples que dans les numérations sur plaque. Les taux d'absorption sont fonction de l'espèce et de la température et ne présentent que peu de corrélation avec les charges bactériennes ambiantes. L'élimination est également fonction de l'espèce et elle est variable.

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The internal bacterial flora of marine bivalves is composed principally of Vibrionaceae and Pseudomonadaceae, but may also include a wide variety of other bacteria, frequently introduced from the environment (Colwell and Liston 1959) and only temporarily held by the bivalve. Most bivalve producing areas are shallow water coastal and estuarine regions, infected with a wide variety of allochthonous bacteria, and many are frequently subjected to sewage pollution. Bivalves are known accumulators and vectors of bacteria pathogenic to human consumers (Ohara et al. 1983). The problem is aggravated by the fact that bivalves are frequently consumed raw, or only partially cooked.

Estimates of accumulation of bacteria and viruses, are based on the use of indicator organisms, notably the nonpathogenic *Escherichia coli*, that is accepted as evidence of faecal contamination (Escherich 1885; Bernard 1973). The relationship of water-borne coliform bacteria and their accumulation by bivalves is a significant factor in the management of bivalve production. An understanding of the dynamics of bacterial uptake and elimination is essential for rationalizing the depuration process, involving transfer of bivalves from polluted to clean seawater, prior to marketing (Quayle and Bernard 1968).

Suspension feeding bivalve mollusks retain small particles from the ventilation stream using the enlarged gill and special adaptations of the mucus cleansing mechanism. Maximum retention occurs with particles >5 μm diameter (Williams 1982), while particles <1 μm diameter are not effectively retained (Winter 1978). Coliform bacteria 3×0.5 μm (Davis et al. 1980) are not efficiently retained, unless aggregated, or attached to larger particles, when they become a significant source of nutrition (Zobell and Feltham 1938). The accumulation of bacteria by bivalves is seasonally variable, and reveals little consistent correlation with the environmental loading. Contemporary public health standards accept a level of less than 2.3 *E. coli* per gram of wet soft tissue as safe for human consumption. While this has not been stringently tested epidemiologically, it is generally accepted (Son and Fleet 1980); however, some pathogens may persist longer in shellfish than *E. coli* (Janssen 1974).

Estimates of numbers of coliform present are determined by geometric serial dilution of water, and bivalve tissue homogenates, to establish a most probable number (MPN). Objections have been raised concerning the reliability of coliform tests (McCarthy et al. 1958). In general, the statistical uncertainties for most probable numbers (MPNs), obtained from multiple-tube fermentation tests, with poor reproducibility, is inferior to the plate count methods. Nevertheless, coliform estimations remain the chief management tool for the protection of public health.

An initial study by Bernard (1970) used suspensions of *E. coli* obtained from gas-positive lauryl tryptose broth, streaked to Levines EMB Agar. The suspensions were dispersed in natural sea water. However, the viability of cultured *E. coli* in seawater suspension differed significantly from that of "natural" effluent from a sewage treatment facility prior to chlori-

[1]Deceased.

nation. The suspension of cultured coliforms also demonstrated wide variations in clearing rates from shellfish and the pattern differed widely from that in naturally polluted shellfish moved to clean water for depuration (Quayle and Bernard 1976). The present study was conducted with untreated dilute sewage and information is presented on the accumulation and elimination of bacteria by four commercial species of bivalves held at three different seawater temperatures.

Materials and Methods

Bivalve samples were obtained from Hammond Bay, on the east coast of southern Vancouver Island. Four representative species were selected and included the Pacific oyster, *Crassostrea gigas*, the bay mussel *Mytilus edulis*, the littleneck clam *Protothaca staminea*, and the steamer clam *Mya arenaria*. The collecting site has low seasonal coliform levels most of the year. Subsamples were tested to establish the original coliform level. The test animals were placed in aquaria supplied with unsterilized water pumped from Departure Bay, and maintained at near seasonal ambient salinity and temperature. Infaunal species were buried in shallow battery jars filled with washed small gravel. Epifaunal species were placed on glass trays.

Untreated diluted sewage from a nearby sewage facility, contained $6.6–20.2 \times 10^6$ coliforms per litre. These values were seasonally stable, so determinations could be made to calculate the necessary dilution with untreated surface seawater to give a suspension of 11–21 MPN/100 mL faecal coliforms after 6 h. This number was selected as representative of slightly polluted waters, just above the public health criteria, and was representative of many shellfish growing areas in British Columbia. The sewage was added to a tank (7000 L, 3-m diameter, 1 m deep) containing surface seawater at 7, 12, and 17°C, filtered through a 500-μm Nitex filter. The suspension was mechanically stirred for 10 min, then maintained by bubbling air into the tank. The tanks were covered with black plastic to reduce bacterial loss from the effect of sunlight. The large tank volume was used to avoid rapid depletion of the coliform suspension during the experiment. Initially, samples of tank seawater were taken at intervals during a 24-h period to assess the effects of temperature and time on coliforms in seawater.

Accumulation experiments were started after a stabilization period of 6 h. Mollusks were added to the tank and 10 individuals sampled hourly, together with the tank water, for 6 h. At the end of the experiments, the tanks were drained, clean water added, and four samples of 10 individuals collected every 2 h, to monitor the coliform elimination pattern during the following 8 h. Other contaminated specimens of *C. gigas* and *M. edulis* were added to clean water at 12°C or held moist in an incubator at 12°C and at intervals up to 24 h samples were taken for analyses.

Coliform enumerations were based on the multiple tube serial dilution in lauryl tryptose broth, followed by the brilliant bile green and EC elevated temperature confirmation tests. All tissue samples, including separate body parts, were processed using standard methods (APHA 1969). Dried meat weights were obtained and used to determine expected ventilatory rates from formulae developed by Bernard (1983), and newly calculated for *M. arenaria* (Table 1). Populations of suspended particles were monitored with a Coulter Counter using the techniques developed by Sheldon and Parsons (1967).

Tests were conducted on plate and MPN counts of stomach juice from *Crassostrea* and *Mytilus* taken from an unpolluted area and held for 10 d in sterilized sea water. A small opening was made in the valve of the shell for insertion of a hypodermic needle to aspirate stomach content which was then filtered through a 2-μm membrane filter. Duplicate standard MacConkey plate counts, and multiple tube estimates were made on tissue homogenates and seawater, one set receiving the gastric juice. Prior to incubation the stomach extract was pipetted onto the surface of the plate and gently swirled and drained.

TABLE 1. Routine ventilatory rates (after Bernard 1983). In the logarithmic curve $Y = a + b \ln X$, a and b are fitted parameters where y is the ventilatory volume (litres per gram per hour) and X is the temperature; r^2 is the coefficient of determination.

Species	a	b	r^2
Mytilus edulis	−0.232	0.923	0.91
Crassostrea gigas	0.553	1.112	0.73
Protothaca staminea	−1.423	1.561	0.89
Mya arenaria[a]	−0.091	1.692	0.83

[a]Newly calculated.

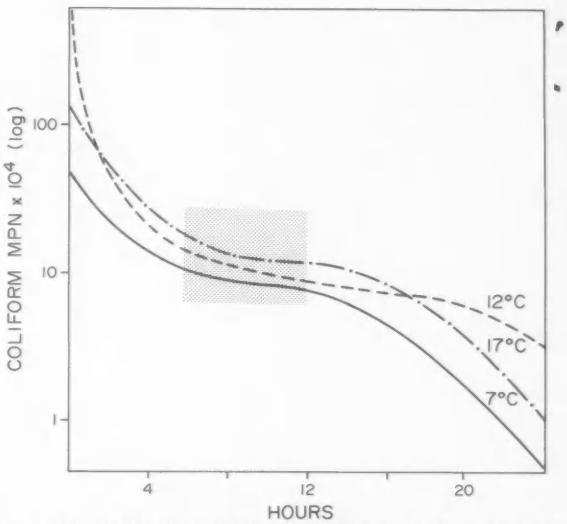

FIG. 1. *E. coli*, Most Probable Number (MPN) counts of experimental tanks at the three temperatures tested. The stippled area shows time of the coliform accumulation experiments.

Results

Behaviour of *E. coli* in Sea Water

Suspensions of untreated sewage plant effluent mixed with surface seawater showed decreasing *E. coli* numbers during the first 5 or 6 h after inoculation into seawater (Fig. 1). This was followed by a stable phase for about 6 h, then coliform numbers decreased slowly for a further 12 h. Temperature probably affected the rate of the initial decrease, with warm water being more bactericidal than cold water (Fig. 1). The ambient MPNs of the three experimental temperatures are shown in Fig. 1, and the coliform accumulation experiments were conducted during the stable phase of coliform bacteria in seawater.

Accumulation of *E. coli*

Patterns of accumulation of coliform bacteria varied with species tested and the temperature of the seawater. *M. edulis*

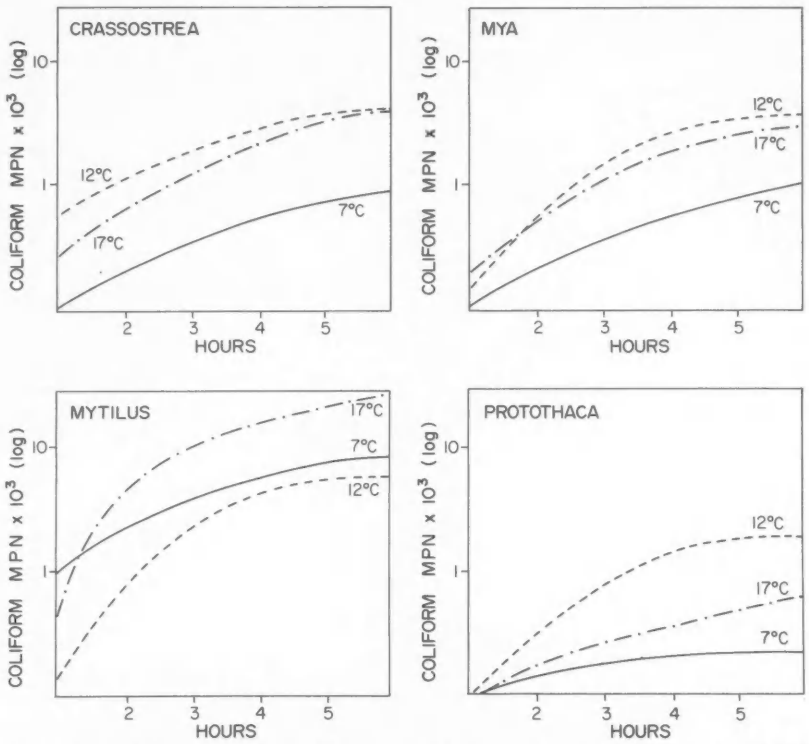

FIG. 2. Accumulation of *E. coli* per g dry meat weight by four species of bivalves at 7, 12, and 17°C.

TABLE 2. Regression constants of accumulation of coliform bacteria (MPN per gram dry weight) by various bivalve species at 17, 12, and 7°C. In the linear equation $Y = a + bX$, a and b are fitted parameters where X is time; r^2 the coefficient of determination.

Species	Temperature (°C)	a	b	r^2
Mya arenaria	17	−275.27	432.17	0.88
	12	−599.13	615.94	0.99
	7	−191.33	167.57	0.99
Protothaca staminea	17	−141.73	100.54	0.90
	12	−363.87	349.49	0.86
	7	−17.60	15.31	0.81
Mytilus edulis	17	−2453.00	4311.86	0.87
	12	−892.73	1062.97	0.84
	7	−204.13	1113.51	0.88
Crassostrea gigas	17	−512.33	641.57	0.99
	12	−82.90	551.80	0.96
	7	−182.13	153.50	0.96

appeared to attain the highest accumulations of coliforms, while only small differences were evident between the other three species, which were positively correlated to temperature (Fig. 2, Table 2).

Combining the results of the four bivalves investigated, there was a positive correlation between coliform accumulation and temperature. The shapes of the temperature specific curves, and the maximum values attained were different. A thermally mediated asymptote after 3–4 h was apparent, probably reflecting digestive action (Fig. 3). The retention of bacteria by bivalves is complex, involving processes both increasing apparent bacterial numbers by accumulation, and decreasing numbers by digestion or sedimentation. Unexpected discrepancies were apparent when the known ventilatory rate and ambient *E. coli* loading were compared with the number in the bivalve. When the uptake process was monitored during the first hour of exposure, the highest counts were in the pallial fluid, which contained pseudofaecal strings. After 2 h the chief depot was the

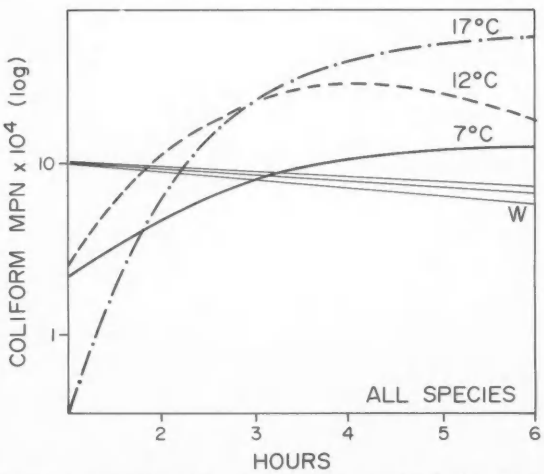

FIG. 3. Accumulation of *E. coli* per g dry meat weight by four species of bivalves combined, as a function of time plotted for 3 temperatures. W = ambient water MPN.

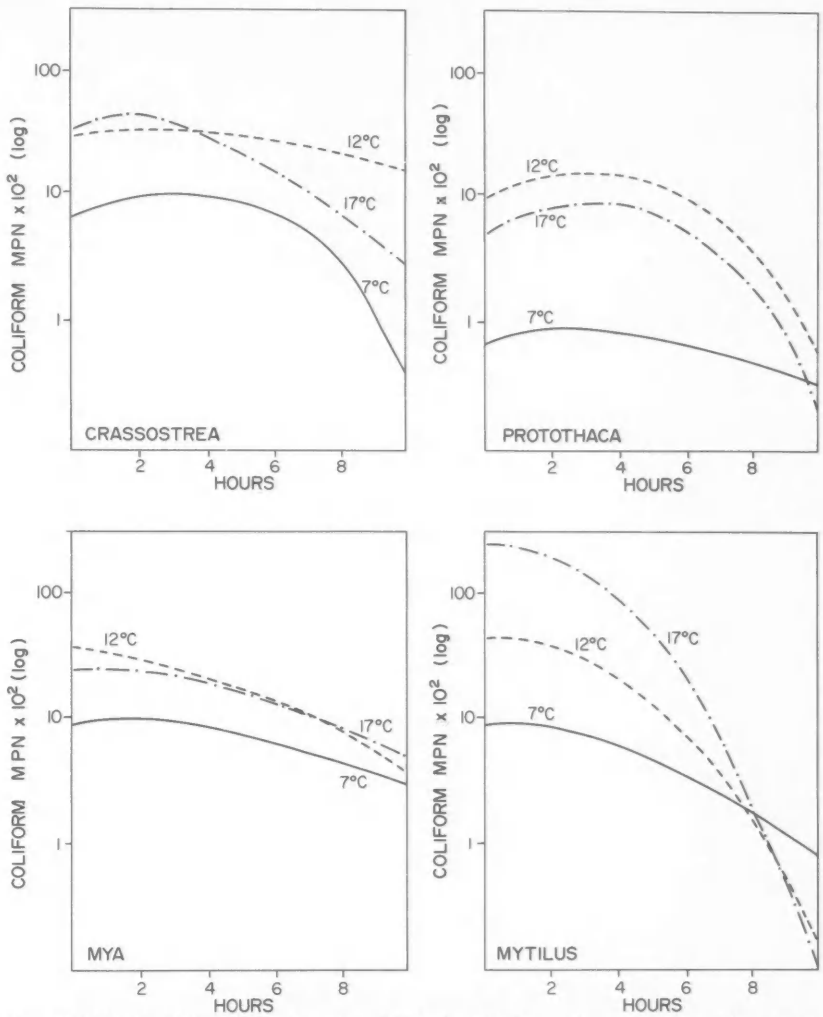

FIG. 4. Elimination of *E. coli* per g dry meat weight by four bivalve species as a function of time plotted for 3 temperatures.

stomach and digestive diverticula. Finally, the bacterial loading moved to the intestine and rectum. Results indicated that shell water with pseudofaeces was transitorily high, and the bacterial concentration was transferred rapidly to the alimentary canal.

Elimination of *E. coli*

Elimination of coliforms was followed in the four bivalves by monitoring meat MPNs at 7, 12, and 17°C. Considerable variation existed in the shape of the curves, both within and between species. Nevertheless, *M. edulis* accumulated coliforms at a higher rate and eliminated them more effectively than the other species (Fig. 4, Table 3).

Role of Gastric Juice on *E. coli* Estimations

Filtered stomach extracts of *C. gigas* increased the number of *E. coli* loci on MacConkey plates, and in multiple tube estimates. All counts of tissue homogenates and seawater were augmented by application of filtered stomach juice, with increases varying from less than three, to 1000 or more. Results from 30 paired tests, using MacConkey plates, yielded a mean of 56 (SD = 67.39) loci for untreated samples, and a mean of 351 (SD = 353.49) for gastric extract treated samples. The difference was significant ($t = -4.68$, $df = 29.0$, $P < 0.05$).

Discussion

Behaviour of *E. coli* in Sea Water

Coliform bacteria enter the marine environment either directly from a point source, usually a sewer outfall, or broadly from river and general run-off. In general bacteria behave like hydrophilic colloids (Vervey and Overbeek 1948), and are subject to coagulation (Duuren 1969).

There exists a wide variation in survival times of coliform organisms in sea water (Greenberg 1956; Orlob 1956), and some

TABLE 3. Regression constants of uniform phase of elimination of coliform bacteria (MPN per gram dry weight) by various bivalve species at 17, 12, and 7°C during routine metabolic rate. In the linear equation $Y = a + bX$, a and b are fitted parameters where X is time; r^2 the coefficient of determination.

Species	Temperature (°C)	a	b	r^2
Mya arenaria	17	3025.50	−261.35	0.97
	12	3554.30	−317.35	0.99
	7	1123.90	−83.35	0.98
Protathaca staminea	17	1297.90	−124.65	0.92
	12	2753.30	−276.40	0.92
	7	104.60	−6.50	0.88
Mytilus edulis	17	25867.78	−3093.60	0.86
	12	4642.32	−531.61	0.91
	7	852.08	−74.02	0.93
Crassostrea gigas	17	5258.10	−535.05	0.94
	12	4208.70	−244.45	0.92
	7	1278.80	−112.00	0.87

workers consider sea water to be intrinsically bactericidal (Carlucci et al. 1961), or inhibitory due to the presence of halogens (Johannesson 1957), as well as various other environmental factors (Buck et al. 1952). Temperature effects have also been implicated (Hanes et al. 1965).

As in the present observations (Fig. 1) dilution in sea water results in a decline in coliform bacteria populations (Mitchell and Chamberlin 1975), probably from the high ionic strength and low nutrient concentration, leading to debilitation rather than death (Dawe and Penrose 1978). Coliform bacteria, however, may persist for extended periods in sea water, and may possibly even multiply (Slanetz and Bartley 1965). The observed initial decline is influenced substantially by the amount and size of suspended particles.

It is known that addition of fine particular matter can reduce suspended bacterial populations by flocculation and that direct sedimentation plays a significant role in removing bacteria. Bacteria adhere to particles, and may thereby gain some ecological advantage and protection. *E. coli* is markedly aggregative and peristatic (Sorokin 1971), so paradoxically the presence of particulate material may reduce the MPN, but prolong viability.

Absorbed bacteria show an increased viability (Rubentschik et al. 1936), and it is likely that absorption, rather than any intrinsic bactericidal factor, is the determinant when survival is considered (Brisou et al. 1964). The dynamic interaction and absorption on particulate material will decrease the apparent number of inocula used as the basis of the standard bacterial enumerative tests. These tests do not discriminate between inocula of a few or many thousand bacteria, and will suggest an actual decrease in total number of bacteria, rather than their continued presence in larger aggregations. There is also a significant negative correlation between the rapid initial decline in sea water with high suspended particle loading and the subsequent stable phase. They may be intercepted by suspension feeding mollusks and be either ingested, or bound in mucous and rejected from the pallial chamber as pseudofaeces. There is significant individual variation in all these processes, and one or the other may dominate, depending on environmental conditions, and the intrinsic physiological condition of the bivalve.

Accumulation of *E. coli*

Accumulation of bacteria by bivalves is a dynamic process and there may be a diurnal pattern present, possibly linked to tidal cycle, in the uptake by oysters (Morton and Shortridge 1976). There also exists marked differences in the rate of bacterial accumulation by the various species (Kueh 1987). These variations are due to differing efficiency of uptake, attributable to morphology of the filter, and varying rates of digestion and elimination. Coliforms present in the bivalve body usually exceed by one or two orders of magnitude the theoretical value obtained by multiplication of the volume of water pumped by the ambient load in the water (Fig. 5). This accumulation "overrun" cannot be explained by direct uptake, and there is little evidence of multiplication of coliform bacteria in shellfish (Kelly and Arcisz 1954). The observations recorded here, show that the high apparent accumulation efficiency of bivalves is probably attributable to the breaking up of bacterial loci, by digestive processes, rather than to any actual change in bacterial absolute numbers. Filtered oyster and mussel gastric juice significantly increases plate and MPN counts of *E. coli* when added to prepared tubes or plates. It is possible that the digestive process of bivalves is responsible for breaking up clumps, leading to increased MPN counts.

Marked temperature and species effects were evident. *Mytilus edulis* accumulated *E. coli* more efficiently at 17°C than at 12 or 7°C (Fig. 2). Interestingly, the lowest accumulation level at 12°C, although probably equivalent initially to the greatest uptake, was considered to result from maximum enzymatic digestion. In the other three species, accumulation was more uniformly related to temperature, but in all cases accumulation was maximal at 12°C, and significantly less at 17°C.

Bacterial accumulation by bivalves is rapid initially, and declines after 3 to 4 h. A plateau phase may be reached, where uptake is equivalent to digestion and pseudofaecal elimination. This is the "steady state" mentioned by many workers, where the number of coliforms taken up is balanced by those eliminated (Cabelli and Heffernan 1970). This equilibrium state, however, is not consistent under natural conditions, and the *E. coli* content in bivalves does not generally reflect the ambient bacterial loading, even when the separation of bacterial clumps by the digestive process is considered. The accumulated coliforms and the load of the overlying water, determined simultaneously at various times of year in British Columbia, have a wide scatter, and no apparent species-specific pattern (Fig. 6, Natural, F. R. Bernard, unpubl. data). Under experimental conditions the relationship improved, and there was a species-specific relationship, with the *Mytilus* most efficient, and *Protothaca* least efficient (Fig. 6, Experiment).

Elimination of *E. coli*

Ingested bacteria may be digested in the stomach and midgut. Others may pass through the intestine while remaining viable (Prieur 1981). A substantial proportion of bacteria are trapped in the cleansing mucus of the pallial cavity and rejected. These bacteria are effectively removed from the water column and are sedimented to the bottom. Bacteriolytic activity in bivalves is well established and lysozyme-like enzymes have been reported in the gut (Seiderer and Robb 1986) and other tissues (McDade and Tripp 1967; Hardy et al. 1976) and may play a role in the utilization of bacteria as a food source. There is also a role for gut microflora in the lysis of bacteria associated with the crystalline style (Seiderer et al. 1987), rather than direct enzymes of the style itself. The majority of bivalves undergo large decreases of coliform bacteria when placed in a clean environment. Monitoring of bacterial counts of bivalves during

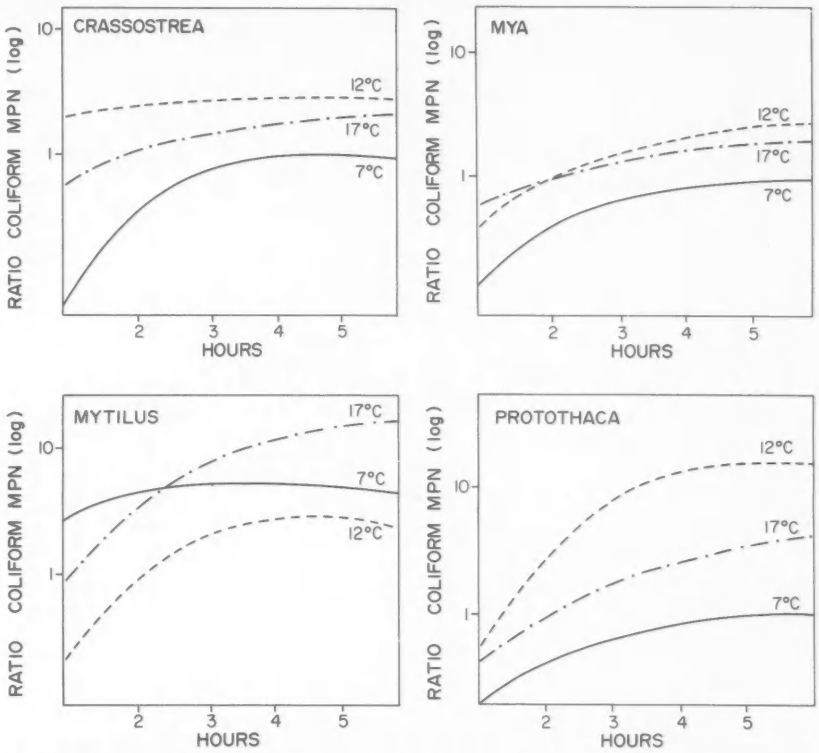

FIG. 5. Ratio of expected to observed *E. coli* MPNs per g dry meat weight for four species of bivalves at various temperatures. Expected values calculated from the ventilatory rates and ambient loading of *E. coli*.

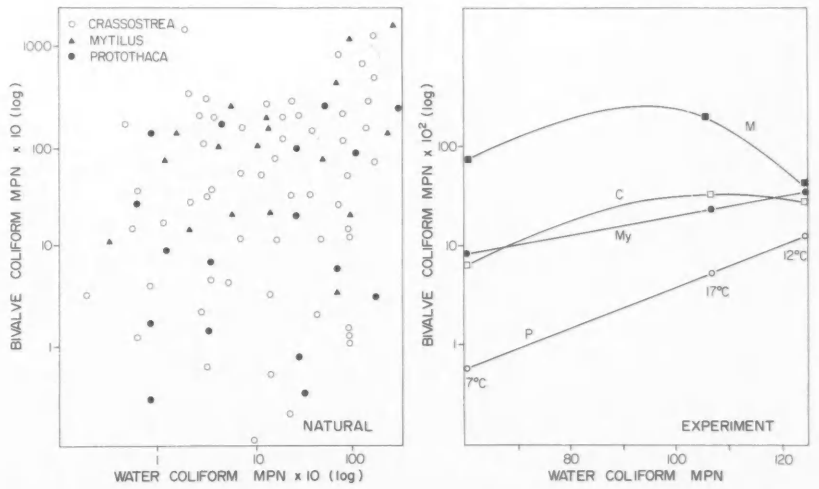

FIG. 6. Scatter diagram of relationship between coliform MPNs in ambient water and various bivalve species (Natural). Relationship between accumulation after 6 hr exposure, and experimental tank loading at various temperatures. C = *Crassostrea gigas*, My = *Mya arenaria*, M = *Mytilus edulis*, P = *Protothaca staminea* (Experiment).

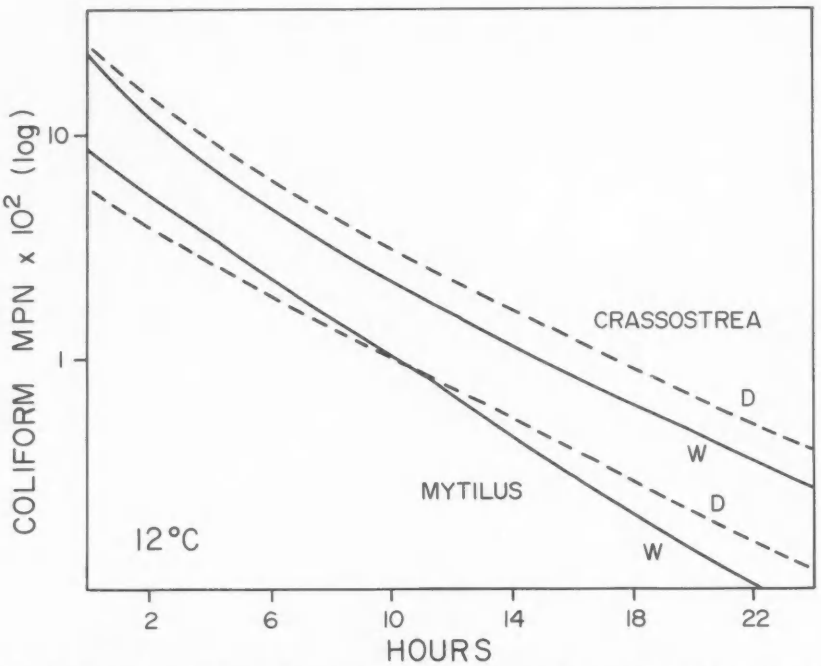

FIG. 7. Elimination of *E. coli* by *Crassostrea gigas* and *Mytilus edulis* during wet (W) and dry (D) storage. Curves calculated using exponential function.

TABLE 4. Regression constants for elimination of coliform bacteria during wet and dry holding of *Crassostrea gigas* and *Mytilus edulis* at 12°C. In the exponential equation $Y = ae^{bX}$, a and b are fitted parameters where X is time; r^2 is the coefficient of determination.

Species		a	b	r^2
Crassostrea gigas	Wet	1473.17	−0.17	0.89
	Dry	1926.02	−0.16	0.91
Mytilus edulis	Wet	865.67	−0.21	0.95
	Dry	506.25	−0.50	0.75

dry storage frequently reveals an initial period of increasing numbers, followed by a decline (Johnson et al. 1973; Son and Fleet 1980).

The present observed patterns of elimination were in substantial agreement with those reported in the literature for various species (see Heffernan and Cabelli 1970, for *Mercenaria mercenaria*). This suggested that the physiological mechanisms of elimination may be similar. In *Crassostrea* and *Protothaca* there were considerable short-term instabilities, usually with maximum MPNs 2 to 4 h after accumulation; *Mya* also revealed a small initial increase. This may have resulted from the break up of bacterial clusters at the commencement of digestion. *Mytilus* had the most direct and efficient elimination curve.

Contrary to the suggestion of Arcisz and Kelly (1955) the ventilation volume exhibited no relationship to rate of bacterial elimination and initial level of accumulation had no influence on length of time to clearance. Comparison over 24 h of elimination of coliform bacteria by *Crassostrea* and *Mytilus*, in clean water or stored dry, showed little difference, if the mantle liquor with the pseudofaeces was eliminated (Fig. 7, Table 4) although the numbers are usually not stable and may fluctuate rather widely (Hoff and Presnell 1963).

Mytilus edulis has bacteriolytic enzymes, lysozymes, in the digestive gland and crystalline style (McHenery and Birbeck 1982), and degradation of bacteria is rapid (Birbeck and McHenery 1982). There are different clearing rates depending on the bacterial species (Janssen 1974). Digestive tract lysozymes capable of digesting bacterial cell walls have been demonstrated (McHenery et al. 1979). The extracellular digestion of bacteria occurs in the stomach, although a proportion of bacteria pass through the digestive tract and remain viable (Cabelli and Heffernan 1970; Prieur 1981). The majority of studies reveal a rapid decrease over 24 h, followed by a much slower decline (Cabelli and Heffernan 1970). At higher temperatures there may be a marked increase of coliform MPN (Hoff et al. 1967).

Acknowledgements

Dr. Frank Bernard died before he could make final revisions to his manuscript, and therefore his colleague Dr. J. N. C. Whyte kindly revised it for him, while I assumed responsibility for subsequent handling. I thank the anonymous reviewers, and Drs. Whyte and D. Quayle, who did final reviews, for their thoughtful comments. While we have tried to revise the manuscirpt in light of these comments as we felt Frank would have done, we may not have been completely successful.

Glen S. Jamieson for Dr. Frank Bernard.

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A Model for Standardizing Dungeness Crab (*Cancer magister*) Catch Rates among Traps which Experienced Different Soak Times

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Smith, B. D., and G. S. Jamieson. 1989. A model for standardizing Dungeness crab (*Cancer magister*) catch rates among traps which experienced different soak times. Can. J. Fish. Aquat. Sci. 46: 1600–1608.

The abundance and size frequency distribution (SFD) of Dungeness crabs (*Cancer magister*) within traps varies with soak time. Such bias in catch rates was reduced using a standardization model that corrected for (1) changes in bait effectiveness over time and (2) agonistic interactions between crabs within traps and those attempting entry. The model estimated the entry and exit of crabs based on the results of trapping experiments specifically designed to (1) emphasize the above two processes and (2) estimate escapement rates from traps for crabs of different sizes. Results clearly indicated the importance of these two processes in modifying trap contents over time, and led to the introduction of the term 'virtual catch rate' (VCR), defined as the rate at which crabs would enter a trap if catch rates did not change with increasing soak time. VCRs are not observed in practice except perhaps for very short soak times, but can be estimated from trap samples by incorporating the aforementioned processes into a standardization model. We found VCR to be a better index of abundance than mean daily catch per trap, and believe it may have utility for other trap fisheries.

L'abondance et la distribution des fréquences de taille du crabe dormeur (*Cancer magister*) d'un casier à l'autre varie en fonction de la durée d'immersion. Pour réduire cette distorsion dans les taux de capture, on a établi un modèle de normalisation qui corrigeait : 1) les changements dans l'efficacité des appâts en fonction du temps et 2) les interactions agonistes entre les crabes présents dans les casiers et ceux qui essayaient d'y entrer. Le modèle estime l'entrée et la sortie des crabes d'après les résultats d'expériences de capture spécialement conçues pour 1) accentuer les deux processus ci-dessus et 2) estimer les taux d'échappement des casiers pour des crabes de différentes tailles. Les résultats indiquent clairement l'importance de ces deux processus dans la modification du contenu des casiers en fonction du temps, et ont amené à la création d'un terme nouveau, «taux de capture virtuel», qui représente le taux auquel les crabes entreraient dans un casier si les taux de capture ne variaient pas en fonction de l'augmentation du temps d'immersion. Les taux de capture virtuels ne sont pas observés dans la réalité, sauf peut-être dans le cas de temps d'immersion très brefs, mais on peut les calculer à partir de l'échantillonnage dans les casiers en intégrant les processus mentionnés plus haut à un modèle de normalisation. Nous avons constaté que le taux de capture virtuel est un meilleur indice d'abondance que la moyenne quotidienne des captures par casier, et nous pensons que ce concept pourrait s'appliquer utilement à d'autres pêches aux casiers.

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Caddy (1979) outlined many factors to consider when using trap sampling data as an index of population density. These include (1) changes in bait effectiveness over time, (2) accessibility of the trap to the target species, (3) trap design and retention capabilities, (4) environmental factors, and (5) behavior of the target species. Such factors cause the size frequency distribution (SFD) and abundance in traps of many marine invertebrates to vary over time, thus making it difficult to accept catch per trap per day as an index of population density. For example, Bennett (1974) demonstrates a dramatic decrease in catch per trap per day with increasing soak time for *Cancer pagurus*. This phenomenon was also reported by Miller (1983) for crabs and lobsters, and by Boutillier (1986) for prawns. Thus, using daily catch rate per trap as an index of population density can be inappropriate if the effect of different soak times on trap samples is not removed (see Somerton and Merritt 1986).

Even if soak times are constant, trap samples can be biased if population densities or SFDs differ among the populations sampled. Interactions between individuals within and outside traps can also influence the population density at which entry and exit are balanced. For crabs attracted to bait such interactions are often agonistic. Miller (1978, 1979) demonstrated that the daily catch per trap of *C. productus* was reduced by agonistic interactions between crabs within traps, and those attempting entry, and Miller (1980) observed agonistic interactions when trapping *C. magister*. By hauling and emptying one set of traps more often than an equivalent set, without changing the bait, he demonstrated that the traps hauled more often caught more crabs. Similarly, Williams and Hill (1982) concluded that the presence of a crab in a trap reduced the probability of further captures of the portunid crab *Scylla serrata*.

We designed experiments to measure (1) changes in bait effectiveness over time, and (2) the effect of agonistic interactions, in order to correct for bias in catch rates. Experiments in 1985 and 1986 were performed at different sites and sampled crab populations with different SFDs. Additional experiments

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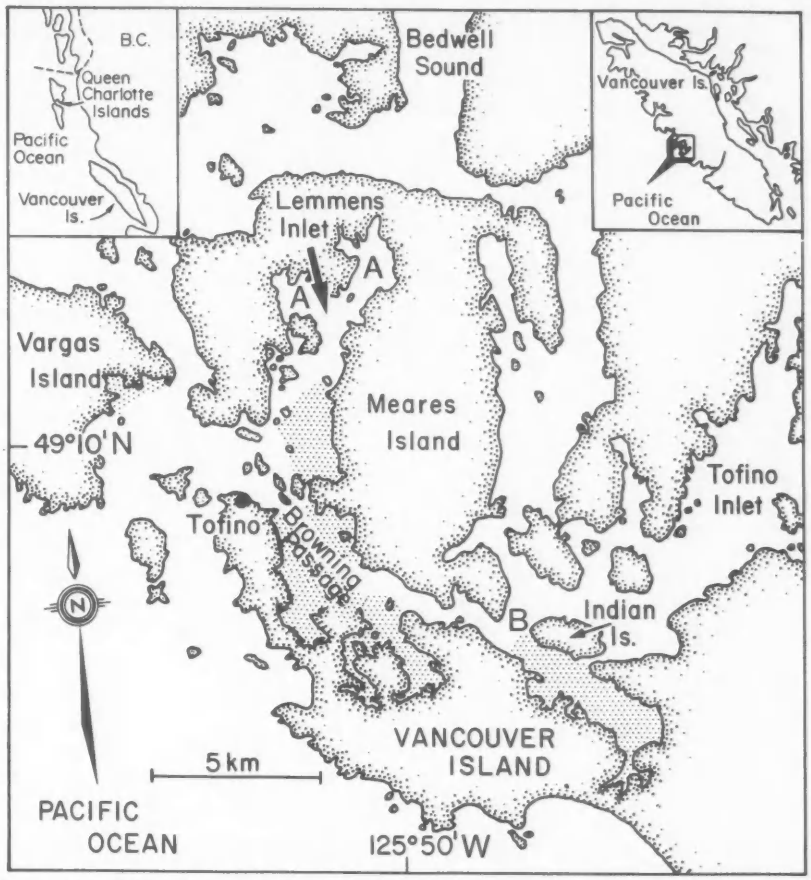

FIG. 1. Map of the waters near Tofino, B.C. showing the experimental sites in upper Lemmens Inlet (A) and near Indian Island (B). Stippled areas are intertidal mudflats.

measured escapement rates for different sizes of crabs by four different trap types. From our results we developed a model to standardize catch data, from which we subsequently estimated the percent exploitation of the Dungeness crab fishery near Tofino, B.C. (Smith and Jamieson 1989).

Site Description

Trapping experiments conducted near Tofino, B.C. (Fig. 1), in 1985 and 1986 were performed in upper Lemmens Inlet and by Indian Island, respectively. Water depth in upper Lemmens Inlet was ≈12 m and the substrate was mud, while near Indian Island the water depth was ≈8 m and the substrate was sand. Annual seawater temperature ranged from ≈6–12°C. Both sites were fished commercially, but the Indian Island site was more typical of commerically fished areas.

Methods

Morphometrics

Relationships were established to determine male and female body lengths from notch-to-notch (i.e. tenth anterolateral spines excluded) carapace widths (CW). Six pairs of measurements were taken for each 1-mm interval from 120–185 and 120–175 mm CW for males and females, respectively. Body length was measured from the tip of the rostrum to the most posterior extension of the abdominal segments in natural position.

Trap Types

The basic commercial Dungeness crab trap (photographs in Miller 1978, 1979) is circular, with stainless steel or rubber-wrapped iron frames 90–105 cm in diameter. Trap height is 25 cm. Iron cross bars give it a weight of 15–25 kg. Diametrically opposed entrance tunnels (21–25 cm wide by 10 cm high) recessed 25 cm from the trap perimeter require crabs to ascend a 20° slope to enter a trap. Two inward-opening one-way triggers prohibit easy exit. Trap frames are covered with a 1-mm stainless steel wire mesh. Bait is placed in the center of the trap in a perforated 500-mL plastic jar; and the bait jar is replaced and the crabs removed by opening a fold-over trap lid normally held shut by a hook on a stretched rubber strap.

Four experimental trap types were distinguished by the number and inside diameter of their escape ports. Escape ports are stainless steel rings welded to the trap frame and are not covered by mesh. They are located high on the side of a trap perpendicular to the entrance tunnels. Paired escape ports are diametrically opposed.

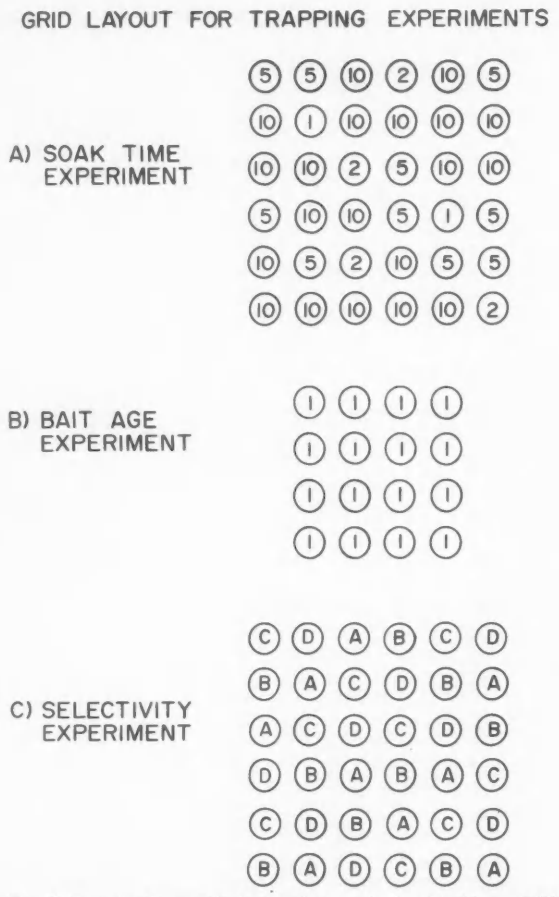
GRID LAYOUT FOR TRAPPING EXPERIMENTS
A) SOAK TIME EXPERIMENT
5 5 10 2 10 5
10 1 10 10 10 10
10 10 2 5 10 10
5 10 10 5 1 5
10 5 2 10 5 5
10 10 10 10 10 2
B) BAIT AGE EXPERIMENT
1 1 1 1
1 1 1 1
1 1 1 1
1 1 1 1
C) SELECTIVITY EXPERIMENT
C D A B C D
B A C D B A
A C D C D B
D B A B A C
C D B A C D
B A D C B A

FIG. 2. Layout of trap grids designed to emphasize the effects of different soak times (A), changes in bait effectiveness (B), and trap selectivity (C) on the abundance and SFD of *C. magister* in traps. For panels (A) and (B), soak times (days) are encircled; for (C), trap type (see methodology) is encircled.

Trap A No escape ports (research traps)
Trap B One 103-mm escape port
Trap C One 109-mm escape port
Trap D Two 109-mm escape ports

Trap A is not legal for commercial fishing but was used in all grid experiments to achieve higher retention of small crabs. Traps B and D are legal for commercial fishing and were used locally by the fishermen whose catch we sampled (Smith and Jamieson 1989). Although not used locally, Trap C is legal and was included in a selectivity experiment to provide an intermediate escapement rate between those of Traps B and D.

Traps used in the following experiments were set in grid patterns (Fig. 2) with the distance between adjacent traps ≈75 m (nominal for the local fishery). We used ≈0.5 kg per trap of geoduck clam (*Panope abrupta* (Randall)) bait, the preference of most local fishermen.

Catch Rates of Traps in Grids

Our fishing experiments generally used a grid sampling format, so we tested the assumption that all traps in a grid were equivalent sampling units by comparing the catch rates of perimeter and interior traps. In July 1985 two five by five grids were arranged in each of the two bays in upper Lemmens Inlet (Fig. 1). After a 24-h soak all traps in both grids were hauled. For each trap in this and all subsequent experiments all crabs caught were sexed, their carapace width measured, and the trap location in the grid recorded.

TABLE 1. Comparison of the mean number of *C. magister* caught per trap for 16 perimeter versus 9 interior traps in two 5 × 5 grids, and between all traps in each grid.

	Mean	SD	Range	Mean	SD	Range	p^a
	Interior			*Perimeter*			
Grid 1	5.7	1.6	5–10	6.5	2.7	3–14	0.48
Grid 2	6.9	2.4	3–10	6.5	3.3	0–12	0.76
	Grid 1			*Grid 2*			
All traps	6.2	2.4	3–10	6.6	2.9	0–14	0.68

[a]Nonsignificant difference of means for all three tests.

Escape of Crabs from Traps

The percent of *C. magister* escaping Trap A in 24 h was estimated by tagging healthy crabs, placing them in a trap, then counting the number remaining after a 24-h soak. After each trap haul, newly captured untagged crabs were tagged and, along with previously tagged crabs, monitored for a successive 24-h period. Crabs were tagged with blue, individually numbered, 4.1-cm anchor tags (Floy Tag and Manufacturing Company, Seattle, WA). Tags were inserted gently through the right posterior epimeral suture line. Crabs with tags that were retained by a trap for 24 h were presumed to represent independent observations for the next 24-h period. For example, observing a tagged crab in a trap for five consecutive days was considered equivalent to having observed five different crabs after 24 h.

Traps were loaded to typical densities (≈5–10 per trap) and placed in a five by five grid in upper Lemmens Inlet, or in pairs near Indian Island. This experiment was performed intermittently from June–August in both 1985 and 1986 with traps being hauled repetitively for up to 10 consecutive days. Performing this experiment in different locations, without changing the bait and 'reusing' tagged crabs, helped reduce biases that might have resulted if only fresh bait, newly captured crabs, or a single site were consistently used. Thus, these escapement rates should be generally applicable to the local commercial fishery.

The selectivities of Traps B–D relative to Trap A were determined by simultaneously fishing nine traps of types A–D in a regular pattern in a six by six grid (Fig. 2c). Each day, for 7 d, all 36 traps were hauled after a 24-h soak, the bait changed, and the traps replaced.

Soak Time Experiment

A six by six grid (Fig. 2a) was used to determine the abundance and SFDs of *C. magister* within Type A traps hauled after soak times of 1, 2, 5 and 10 d. This grid was arranged in upper Lemmens Inlet in August 1985 and near Indian Island in June 1986. Twenty hauls were made for each soak time trial by hauling the appropriate traps on 10 consecutive days according to the following schedule. Trap locations within the grid for the various soak times were chosen randomly. After each

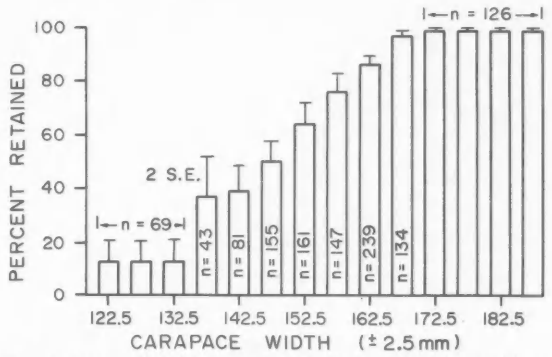

FIG. 3. Percent of male *C. magister* retained by Trap A for 24 h as a function of CW. Males 120–135 and 170–190 mm CW were combined into larger intervals of 15 and 20 mm, respectively, because of small sample sizes and no apparent differences in escapement over these size ranges.

trap haul all crabs were released, the bait changed, and the traps replaced where they were hauled.

Two 1-d soak traps hauled every day.
Four 2-d soak traps hauled every second day.
Ten 5-d soak traps hauled every 5 d.
Twenty 10-d soak traps hauled after 10 d.

A separate five by four grid was arranged and fished in the same location 20 d prior to the grid just described in order to provide 20 replicates for a 20-d soak. This trial was repeated after the shorter soak time trials to assess any trend in the catch rate over time. No difference in catch rate was evident, so results from the first trials were used in the analyses of both the 1985 and 1986 experiments.

Bait-Effectiveness Experiment

Changes in the abundance and SFDs of crabs within Trap A resulting from changes in bait effectiveness were assessed in a four by four grid (Fig. 2b) over the same 10-d period as the 1-, 2-, 5-, and 10-d soak time trials. In upper Lemmens Inlet the soak time and bait effectiveness experiments were 2 km apart, with one grid in each bay. The two grids by Indian Island were ≈200 m apart. At the beginning of the experiment all 16 traps were set with fresh bait, then every 24 h, for eight consecutive days, all 16 traps were hauled, the crabs released, and the traps replaced without changing the bait. On the ninth day the bait jar was removed and the traps were fished without bait.

Experimental Results

Morphometrics

Linear relationships between notch-to-notch carapace width (CW, millimetres) and body length (L, millimetres) were established for the carapace width ranges of 120–185 mm and 120–175 mm, for male and female *C. magister*, respectively. Males:

(1) $L = 4.95 + 0.677(CW)$; $r^2 = 0.984$, $n = 390$

Females:

(2) $L = 1.94 + 0.718(CW)$; $r^2 = 0.975$, $n = 330$.

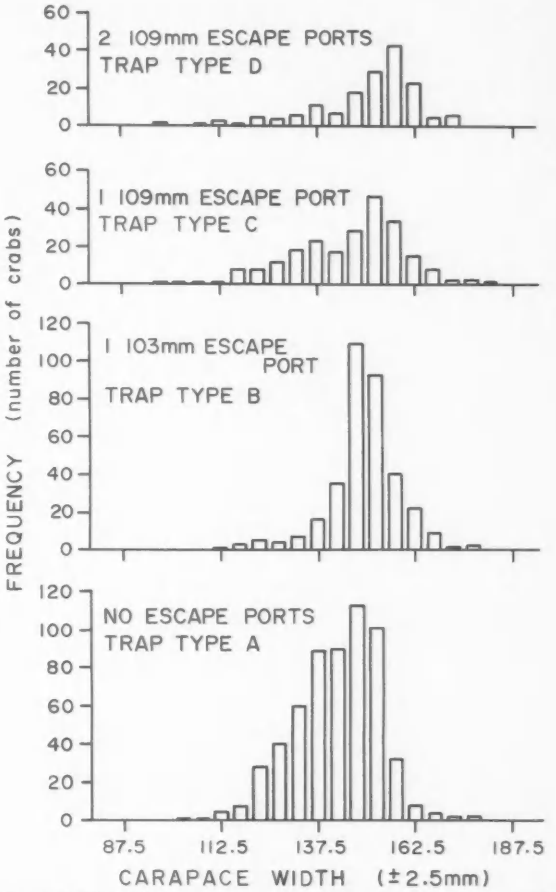

FIG. 4. SFDs of *C. magister* caught in nine traps each of types A–D after a 24-h soak.

Catch Rate of Traps in Grids

Numbers of crabs caught per trap were similar within and between grids (ANOVA, $p > 0.1$, Table 1), and the distribution of the numer of crabs per trap did not deviate significantly from a normal distribution (Kolmogorov–Smirnov, $p > 0.1$). Also, the distribution of the number of crabs per trap was not significantly ($p > 0.1$) different for interior versus perimeter traps in either grid. Consequently, we considered each trap to be an independent sampling unit.

Escape of Crabs from Traps

Figure 3 shows Trap A (research traps) to be ineffective in retaining male crabs <135 mm CW, undoubtedly because they easily enter and exit traps through the mesh. Between 135–170 mm CW increasing retention (P, percent) with CW is described by equation (3), estimated by a weighted least-squares regression, i.e. the deviation of a predicted and measured data pair (P, CW) was divided by the standard deviation of P. Crabs >170 mm CW are effectively retained. (No data are presented for females because too few records were obtained due to their lower abundance and smaller size.)

(3) $P = 2.24(CW) - 2.78$.

TABLE 2. Retention of crabs <155-mm CW for Traps C–D, and crabs <145-mm CW for Trap B, relative to Trap A. The relative retention for a trap type is the number of crabs caught by that trap type divided by the number caught by Trap A after equivalent soaks (N_j/N_A). For Trap A, $n = 536$ for crabs <155-mm CW, and $n = 322$ for crabs <145-mm CW.

Trap	n	Relative retention	SD
B	71	0.220	0.023
C	164	0.306	0.020
D	87	0.162	0.016

TABLE 3. Probabilities of male *C. magister* being retained by Traps A–D for 24 h.

Carapace width (mm)	Trap			
	A	B	C	D
120–125	.130	<.001	<.001	<.001
125–130	.130	<.001	<.001	<.001
130–135	.192	<.001	<.001	<.001
135–140	.304	<.001	<.001	<.001
140–145	.416	<.001	.007	<.001
145–150	.529	.529	.012	<.001
150–155	.641	.641	.019	<.001
155–160	.753	.753	.753	.753
160–165	.866	.866	.866	.866
165–170	.978	.978	.978	.978
>170	.992	.992	.992	.992

Figure 4 shows SFDs for the total catch by nine traps each of trap types A–D fished simultaneously for 7 d. Carapace widths for females were expressed as male-equivalent CW for the same body lengths using equations (1) and (2). Since escapement rates are determined largely by the ability of a crab to walk sideways out an escape port, the important measurement in this regard is body length.

There were no remarkable differences in retention of crabs >155 mm CW among Traps A–D, so the percent retained by Trap A was assumed to apply to Traps B–D. For Trap B, this assumption was extended to crabs >145 mm CW. Carapace widths of 145 and 155 mm correspond to body lengths of 103 and 110 mm, which are close to the escape port diameters for Traps B (103 mm) and C–D (109 mm), respectively, thus supporting the contention that retention rates are mainly determined by escape port diameter. However, the relationship between crab size and escapement rate is clearly more complex since Trap C, with one 109-mm escape port, apparently retains smaller crabs more effectively than Trap B, with one 103-mm escape port (Fig. 4). Presumably escapement estimates are biased to some degree by differences in entry rates, agonistic interactions, and other factors.

For crabs <155 mm (Traps C–D) and <145 mm (Trap B), the percent retained was determined by solving equation (4) (see next section for source) for X_i using the ratio of $N_j{:}N_A$ (j = B,C,D) for Traps B–D relative to Trap A. The ratio $N_j{:}N_A$ was determined by comparing the abundance of crabs in Traps B–D (N_j) relative to Trap A (N_A) after a 1-d soak ($T = 1$) (Table 2). The virtual catch rate (V_i, see next section) was assumed equal for all trap types; and X_i for Trap A was estimated from Fig. 3 and equation (3).

$$(4)\quad N_j/N_A = (V_i/X_i)(1 - \exp[-X_iT]),$$

where V_i is the virtual catch rate per trap for a crab in carapace interval i, X_i is the $-\ln$(daily probability of a crab in carapace interval i being retained by that particular trap type).

Table 3 reports daily retention probabilities for males 120–170+ mm CW for Traps A–D. Only Trap A was used in the soak time and bait-effectiveness experiments, but results for Traps B–D are reported because they were used when standardizing commercial samples (Smith and Jamieson 1989).

Standardization Model

Development

Our model predicted the abundance and SFD of *C. magister* within type A traps which experienced different soak times and bait ages, with the predicted number of crabs in a trap being a function of entry and escapement rates, agonistic interactions, and changes in bait effectiveness over time. For each 5-mm CW interval we defined 'virtual catch rate' (VCR) as the number of crabs that would enter a trap each day if (1) bait effectiveness did not decrease over time, and (2) crabs within a trap had no effect on catch rate. A vector of 20 (in 1985) and 18 (in 1986) unknown parameters represented the VCRs for each 5-mm CW interval between 90–200 mm CW where at least one crab was sampled. As previously explained, female carapace widths were converted to male-equivalent carapace widths for the same body lengths.

Equation (5) describes the net daily change in the number of crabs in a trap as a function of entry and exit rates.

$$(5)\quad dN_i/dt = V_iR_1R_2 - X_iN_i,$$

where N_i is the number of crabs in carapace interval i in a trap, t is the time interval in days, V_i is the daily VCR for crabs in carapace interval i, X_i is the $-\ln$(daily probability of a crab in carapace interval i being retained by Trap A) (from Table 3), R_1 is the relative effect of agonistic interactions, and R_2 is the relative effect of changes in bait effectiveness.

In theory, VCRs are not achieved for any soak time because bait deterioration and agonistic interactions begin as soon as a trap is placed in the water. Therefore, four variants of equation (5) were tested on their ability to model the entry and exit of crabs into and out of traps for the duration of the soak time and bait-effectiveness experiments. These variants presumed (1) no agonistic effects or changes in bait effectiveness over time, (2) agonistic effects alone, (3) changes in bait effectiveness alone, and (4) both (2) and (3) above. If one assumes that bait effectiveness does not change over time, and there are no agonistic interactions among crabs, then $R_1 = 1$ and $R_2 = 1$ and equation (5) can be integrated from time = 0 to T by equation (6). (See Ricker 1975, pages 14 and 15, for an analogous derivation.)

$$(6)\quad N_i = (V_i/X_i)(1 - \exp[-X_iT]).$$

Alternatively, R_1 and R_2 vary from 0–1 decreasing observed catch rates as a result of agonistic interactions and changes in bait effectiveness, respectively. When $R_1 < 1$ or $R_2 < 1$, then equation (5) cannot be readily integrated, so the predicted number of crabs in a trap at any time was determined using the Runge–Kutta method of numerical integration (Boyce and DiPrima 1977).

Equation (7) defines R_1, i.e. the relative effectiveness of trapped crabs in reducing further entry of crabs. This formulation is based on the results of competition experiments

TABLE 4. Comparison of different models explaining the abundance and SFDs of *C. magister* in sets of traps which experienced different soak times and bait ages during equivalent experiments in 1985 and 1986. The objective function (A) is the separation statistic of Schnute and Fournier (1980). P is the number of parameters in the model. AIC (see text) measures model performance and parsimony, the lower the value the more likely the model.

	1985			1986		
Model	A	P	AIC	A	P	AIC
1. Constant entry rates[a]	657	20	697	736	18	772
2. Agonistic-interactions[b]	433	22	477	549	20	589
3. Bait-effectiveness[c]	601	22	645	545	20	585
4. (2) and (3) above[d]	422	24	470	469	22	513

[a]Same entry rate over time for each 5-mm CW interval. Number of crabs in a trap increases asymptotically. Equation (5) with $R_1 = 1$ and $R_2 = 1$).

[b]Different entry rates and SFDs over time (equations (5) and (7), $R_1 < 1$, $R_2 = 1$).

[c]Different entry rates over time (equations (5) and (9), $R_1 = 1$, $R_2 < 1$).

[d]Different entry rates and SFDs over time (equations (5), (7), and (9), $R_1 < 1$ and $R_2 < 1$).

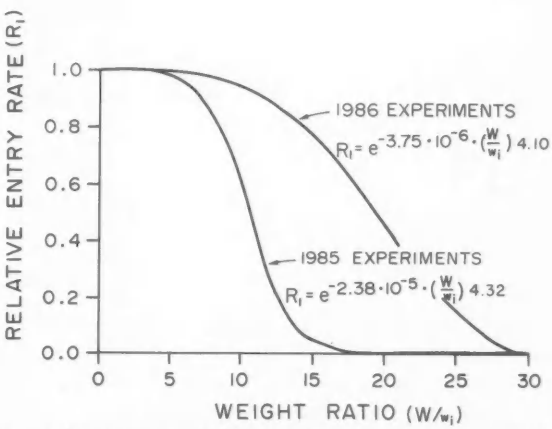

FIG. 5. Relative rate at which *C. magister* enter Trap A as a function of the ratio between the total weight of crabs in a trap and the weight of the crab attempting to enter the trap. This plot uses the best parameter estimates for equation (7) from Model 4 (Table 4).

(Scrivener 1971) which showed that even small differences in the relative sizes of two contesting American lobsters (*Homarus americanus*) nearly assured the larger lobster of winning. For example, a legal-sized lobster with a carapace length 5% larger than its competitor won ≈90% of encounters, i.e. the loser backed away.

(7) $R_1 = \exp[-a(W/w_i)^b]$,

where R_1 is the relative entry rate into a trap for a crab of weight w_i in carapace interval i, W is the total weight of crabs in a trap, a is the instantaneous rate of decrease in the entry rate of a crab as a function of the 'weight-effect' ratio (W/w_i), and b allows the weight-effect ratio to assume a nonlinear form.

A crab's competitive ability was represented by its weight, thus we assumed that competing individuals interpret their competitor's combative prowess by relative size, e.g. claw size (Scrivener 1971; Atema and Cobb 1980). In the special case of

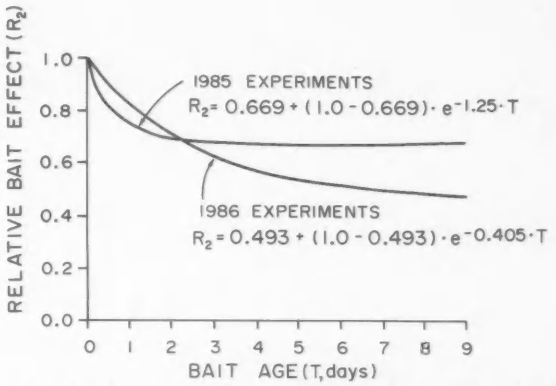

FIG. 6. Relative entry rate of *C. magister* into Trap A as a function of bait age. This plot uses the best parameter estimates for equation (9) from Model 4 (Table 4).

agonistic interactions between crabs within and outside traps, the weight of crabs within a trap is a proxy for the relative competitive ability of trapped crabs in aggregate. This is an imperfect representation of relative competitiveness; however, other one and two parameter models based on numbers and/or weight as a measure of relative competitive ability were less capable of explaining the data. Dry weight (w, grams) for males and females was determined from its relationship to CW as defined by Stevens and Armstrong (1984).

(8) $w = 0.0000863(\mathrm{CW})^{2.832}$.

Equation (9) defines R_2, i.e. the relative change in bait effectiveness with increasing bait age. It assumes a base rate at which crabs are attracted to traps in the absence of bait (s), plus a complementary component ($1 - s$) which has a maximum ability to attract crabs at $T = 0$ and declines exponentially (q) with time (T).

(9) $R_2 = s + (1 - s)\exp[-qT]$.

Model Results

The two experiments enhancing the effects of soak time and bait-effectiveness were both unavoidably influenced by soak time and changes in bait effectiveness. However, both experiments sampled the same *C. magister* population, so we assumed similar parameter estimates for both experiments, and estimated VCRs simultaneously for both experiments. Parameter estimates were obtained separately for the 1985 and 1986 experiments using the nonlinear estimation package of Mittertreiner and Schnute (1985). A maximum likelihood objective function, the separation statistic A of Schnute and Fournier (1980), was minimized to obtain the parameter estimates. Akaike's Information Criterion (AIC) (Akaike 1974), which equals A plus twice the number of model parameters, was used to judge overall model performance and parsimony, with the lowest value indicating the most likely model.

Table 4 lists A and AIC for the four variants of the general model. In both 1985 and 1986, Model 4, which includes both bait-effectiveness and agonistic processes, outperformed all other models. These two processes explained considerable variability in the abundance and SFD of crabs among the experimental treatments. However, in 1985, the effects of agonistic

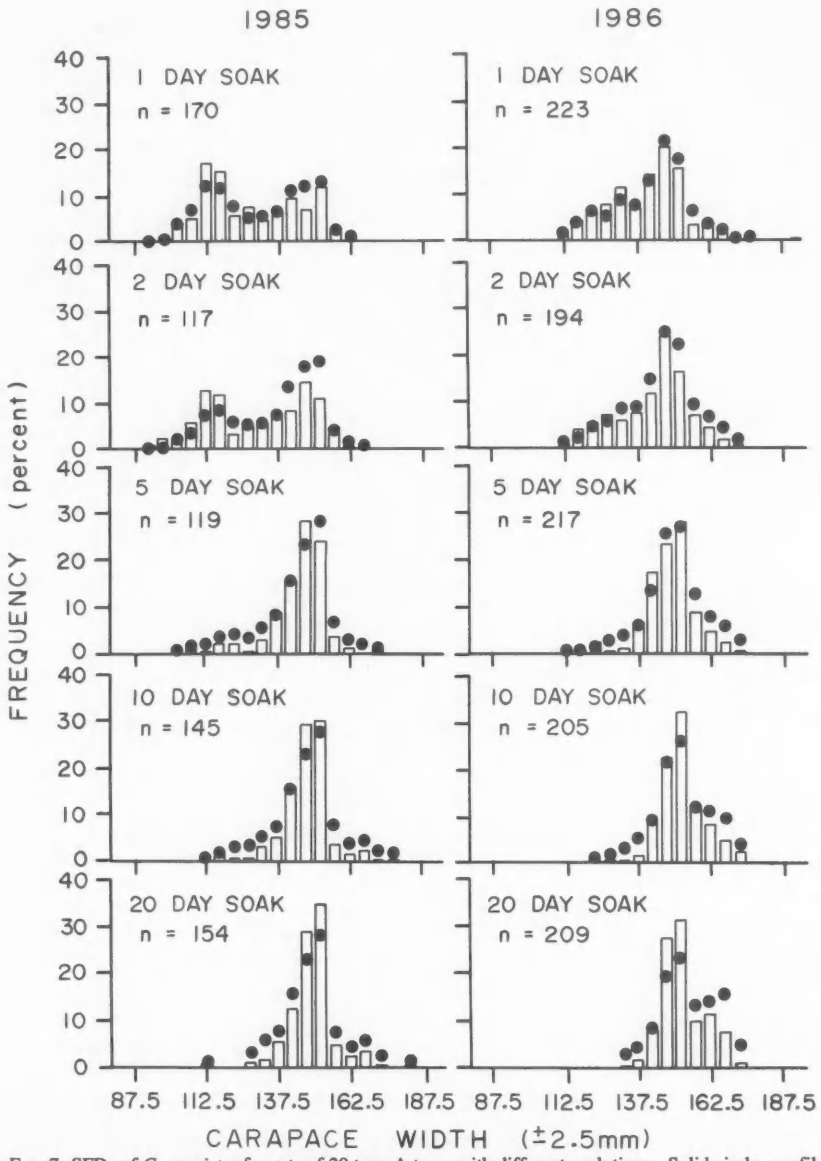

FIG. 7. SFDs of *C. magister* for sets of 20 type A traps with different soak times. Solid circles profile predicted SFDs using the best parameter estimates from Model 4 (Table 4).

interactions were clearly dominant over changes in bait effectiveness. Since the model was structured to produce a SFD of VCRs, estimation of a covariance matrix was precluded by high correlations among parameters, and parameter estimates lying near constraints (i.e. VCRs near 0). Use of resampling methodology (Efron 1982) was prohibited by computer time limitations.

Differences in parameter estimates for the agonistic-interactions equation (equation (7), Fig. 5) in both the 1985 and 1986 experiments may reflect differences in crab SFDs between 1985 and 1986. Equation (7) cannot account for size-dependent biases in the relative competitiveness of *C. magister* individuals, so the higher density of smaller crabs in 1985 might have resulted in parameter estimates different from those obtained in 1986. Forty-four percent of the 1602 crabs captured in the 1985 experiments were <130 mm CW, compared with only 15% of the 2220 crabs captured in 1986. Traps are ineffective in retaining crabs <135-mm CW so the different parameter estimates may also reflect poor escapement estimates for small crabs.

Differences in parameter estimates for the bait-effectiveness equation (equation (9), Fig. 6) between 1985 and 1986 may be due to differences between habitats. The 1985 experiments were performed in a 12-m deep, low current area in upper Lemmens Inlet, whereas the 1986 experiments were performed in 8-m-deep, well-mixed water near Indian Island. Relative bait effectiveness probably diminished less rapidly near Indian Island

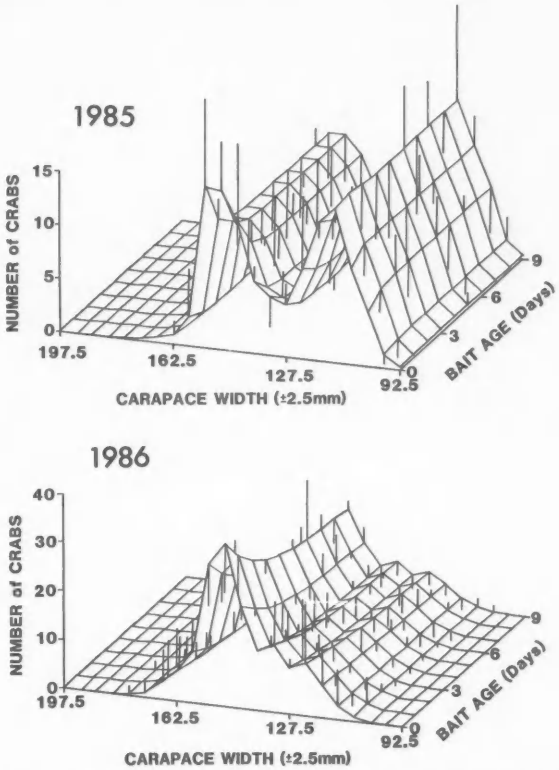

FIG. 8. Response surface of predicted SFDs of *C. magister* within 10 sets of 16 type A traps used in the bait effectiveness experiments. Vertical lines show the observed data point when the difference between the observed and predicted point is greater than one. These results use the best parameter estimates from Model 4 (Table 4).

because good flushing of the bait produced an effective odour trail. In upper Lemmens Inlet there was little current to produce an effective odour trail once the bait juices dissipated after 1 or 2 d. Further, the small crabs caught in 1985 may have used traps for refuge, thus yielding a high catch rate in the absence of bait.

A reduced catch rate, and fewer small crabs, with increasing soak time is evident for both the 1985 and 1986 experiments (Fig. 7). The decrease in bait effectiveness over time (Fig. 6) is not particularly apparent in Fig. 8 due to the confounding effects of agonistic interactions and escapement. Figure 8 shows that the residuals are not completely random for either the soak time or bait-effectiveness experiments. This may indicate: (1) poor escapement estimates for particular carapace width intervals, (2) the influence of tides, currents or other interventions, (3) imperfect understanding of agonistic-interactions and bait-effectiveness processes, (4) patchiness in crab distributions, and/or (5) the presence of unidentified processes. In particular, the theoretical suitability of the agonistic-interactions equation is difficult to evaluate since little is known about the dynamics of agonistic interactions, and the formulation used only summarizes the net effect of agonistic processes.

Discussion

Modelling (1) agonistic interactions, (2) changes in bait effectiveness, and (3) escapement helped standardize our estimates of catch rates and SFDs from *C. magister* trap samples. However, we do not presume that our model fully explains the dynamic interactions between *C. magister* and traps since tides, currents, temperature, photoperiod, and seasonal changes in dynamics were not studied; and females were assumed to have the same dynamics as males. Nevertheless, we anticipate that the concept of VCR can have application in trap fisheries where abundance and SFD information deteriorates over time due to various processes. It is not essential that such processes be fully understood (e.g. we lack that understanding for agonistic interactions), rather it is only necessary that the functional form of the processes be recognized and an appropriate empirical relationshp established. We of course recognize that this can limit the general applicability of a particular model, and such a limitation applies to our model.

We found VCR to be an adequate index of abundance for our application (Smith and Jamieson 1989), but VCR remains biased by many factors. If different-sized crabs move at different rates, some will be less likely to encounter a trap than others, and thus may be undersampled. For example, Miller (1975) observed that immature and female *Chionoecetes opilio* were aggregated, whereas mature males were apparently randomly distributed. Further, the standardization model does not consider agonistic interactions among crabs outside (or inside) a trap, where smaller crabs would be expected to be weak competitors versus larger crabs. Miller (1978) observed agonistic interactions between individuals of *C. productus* around the outside of a trap.

Another important consideration is that as soak time increases, information on smaller crabs is lost because they readily escape and are excluded from traps by the increasing number of larger crabs retained (Fig. 7). Thus, when catch rates and SFDs for samples with longer soak times are standardized, the results for smaller crabs will become less reliable. For these reasons our standardization model was used cautiously, and in Smith and Jamieson (1989) we rejected samples where the soak times exceeded 10 d; and we trusted the model only for crabs >145-mm CW.

A standardization model such as ours may not be necessary when samples have equal and short soak times. Figure 7 suggests SFDs are fairly stable for 1- and 2-d soaks in both the 1985 and 1986 experiments, so mean daily catch per trap may be a reliable index of abundance for short soak times. Most of the samples analyzed in Smith and Jamieson (1989) were obtained from commercial fishing vessels and soak times could not be controlled. When possible, researchers would be wise to avoid the interpretation problems associated with long and variable soak times, since extensive field experimentation and computer time may be required to develop a reliable standardization model.

Acknowledgments

The skill and wisdom of the technical staff at Pacific Biological Station ensured a productive, effective, and enjoyable field program. We especially thank W. Carolsfeld, W. Harling, D. Heritage, A. Phillips, and their student assistants for assuring efficient and safe field work. This work was performed while B. D. Smith was supported by a Department of Fisheries and Oceans Postgraduate Scholarship from the Biological Sciences Branch.

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Exploitation and Mortality of Male Dungeness Crabs (*Cancer magister*) Near Tofino, British Columbia

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Smith, B. D., and G. S. Jamieson. 1989. Exploitation and mortality of male Dungeness crabs (*Cancer magister*) near Tofino, British Columbia. Can. J. Fish. Aquat. Sci. 46: 1609–1614.

Male Dungeness crabs (*Cancer magister*) were sampled by traps and monitored by tagging as they moulted and entered the fishery near Tofino, British Columbia, from April 1985 until March 1987. Males first recruited to the fishery after moulting from the $\mu = 129$-mm CW (carapace width) to the $\mu = 156$-mm CW normal instar. Sublegal-sized males (<154 mm notch-to-notch CW) in the $\mu = 156$-mm CW instar (≈42% of this instar) were found to have a high annual natural mortality ($M = 2.9$–4.5), with <10% surviving to legal size. Legal-sized males experienced high annual fishing mortality ($F = 5.1$–6.9), so consequently a small component of the commercial catch consisted of males in larger instars. Size frequency analysis, which measured the percent exploitation of the $\mu = 156$-mm CW instar, indicated that legal-sized males remained in relatively low abundance during this year-round fishery because of intense exploitation. Mark–recovery data and size frequency analysis also indicated this intense fishery was sustained throughout most of the year by a protracted moulting season. Consequently, we observed prolonged periods with a high percentage of less desirable soft-shelled males in the commercial catch.

Les crabes dormeurs mâles (*Cancer magister*) ont fait l'objet d'un échantillonnage au casier et d'une surveillance par marquage au moment de la mue et de l'entrée dans la phase exploitable près de Tofino (Colombie-Britannique), entre avril 1985 et mars 1987. Les mâles entraient en phase de recrutement après la mue où ils passaient de la phase $\mu = 129$ mm de largeur de la carapace (LC) à la phase normale $\mu = 156$ mm LC. Les mâles de taille inférieure à la taille légale (<154 mm LC d'une encoche à l'autre) dans la phase $\mu = 156$ mm LC (≈42 % de cette phase) présentaient une forte mortalité naturelle annuelle (M = 2,9–4,5), avec «10 % survivant jusqu'à la taille légale. Les mâles de taille légale présentaient une forte mortalité par pêche annuelle (F = 5,1–6,9), de sorte qu'une faible proportion seulement des prises commerciales se composait de mâles de grande taille. L'analyse de la fréquence par taille, qui mesurait le pourcentage d'exploitation des crabes de la phase $\mu = 156$ mm CL, indiquait que les crabes de taille légale restaient relativement peu abondants pendant la saison de pêche, qui dure toute l'année, à cause de l'exploitation intense qu'ils subissent. Les données sur la récupération des marques et l'analyse des fréquences de taille ont aussi indiqué que cette pêche intense était soutenue pendant la plus grande partie de l'année par l'étirement de la saison de mue. Nous avons donc observé des périodes prolongées pendant lesquelles les prises commerciales présentaient un fort pourcentage de mâles à carapace molle, qui sont peu recherchés.

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Dungeness crabs (*Cancer magister*) are commercially exploited using traps in several regional fisheries in British Columbia (Jamieson 1985). While both males and females greater than the minimum legal size limit can be legally retained, females are rarely retained because few reach legal size, fishermen believe it is poor conservation policy, and the market prefers males. There have been no yield- or eggs-per-recruit analyses of the minimum legal size limit for *C. magister* because reliable estimates of growth and mortality have not been available (Methot 1986). This information gap has also inhibited some population models proposed to explain cyclic landing statistics in Washington, Oregon, and California (Botsford 1986).

The purpose of our study was to estimate natural and fishing mortalities, and percent exploitation, for the Dungeness crab fishery near Tofino, B.C. We specifically followed sublegal-sized males for 18 mo during which time they moulted and recruited to the fishery at 154 mm notch-to-notch (= 165 mm spine-to-spine) carapace width (CW). Information on natural and fishing mortalities, and the pattern of recruitment to the fishery, was gathered from a mark–recovery program. The percent exploitation of legal-sized males was estimated by size frequency analysis (SFA) on samples from commercial and research traps, using instar carapace width means (μ) and standard deviations (σ) estimated by SFA on independent samples collected by beam trawl (Smith and Jamieson 1989b).

Trap samples generally yield abundance and size frequency data biased by the dynamics of entry and exit of crabs. Additionally, changes in bait effectiveness over time, and agonistic interactions between crabs within and outside traps, create sampling bias (Caddy 1979). We therefore standardized the catch rates and size frequency distributions (SFDs) obtained from trap samples which experienced different soak times using the model described in a companion paper (Smith and Jamieson 1989a). In that paper we introduced the concept of a 'virtual catch rate', an index of abundance we found superior to mean daily catch

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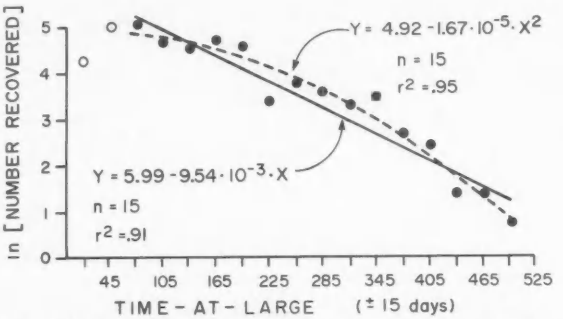

FIG. 1. Linear and quadratic regressions of recoveries over time for tagged male *C. magister* released and recovered as sublegal-sized crabs 145–155-mm CW. Most tagging was done from May–July 1985, and recoveries were by authors and by fishermen (see methods). Data points indicated by open circles were not included in the regression analyses because fishermen had not been well prepared for the mark–recovery program at this time.

rate per trap, and which we employ in this paper. The virtual catch rate is the rate crabs would enter a trap if entry rates were not modified by bait effectiveness, agonistic interactions, and other factors that change with increasing soak time.

Study Site

The waters near Tofino on the west coast of Vancouver Island are shallow (≈5–15 m depth) and well mixed, with annual temperature ranging from ≈6–12°C. Our study site (see figure 1 of Smith and Jamieson 1989a) included ≈15 km around Tofino and was within the Canadian Department of Fisheries and Oceans Statistical Area (SA) 24. Twenty-seven and 59 vessels reported landings from SA 24 during 1985 and 1986, respectively. Of the latter vessels, 30 are known to have fished in the study area in 1986, and they accounted for ≈80% of the 265 t of *C. magister* landed from SA 24 in 1986. The fishery was open and exploited year-round.

Methods

Trap Sampling

We sampled *C. magister* catch on board four commercial vessels at approximately monthly intervals from April 1985 until September 1986. These abundance and SFD data were complemented by data from research traps which we fished over the same time period. Research traps were similar to commercial traps but lacked escape ports, so they helped us assess the abundance of smaller crabs. In total, three trap types, differing mainly in the inside diameter of their escape ports, were used in this study; trap types A, B, and D of Smith and Jamieson (1989a).

Mark–Recovery

Legal- (>154-mm CW) and sublegal-sized male *C. magister* were trap caught, tagged, and released between April 1985 and May 1986. About 89% of the releases were in Lemmens Inlet, 6% were near Indian Island and the remainder were scattered throughout the study area. Pertinent details of the schedule and number of releases appear in the results section. Each crab was sexed and its notch-to-notch carapace width measured (rounded down to the nearest millimetre) before being released, and the date, location, and tag number were recorded. Individually numbered 4.1-cm T-bar anchor tags (Floy Tag and Manufacturing Company, Seattle, WA) were inserted through the right posterior epimeral suture line with a tagging gun, taking care not to puncture internal organs. Blue tags were used because the fishermen believed blue contrasted well against the natural colour of *C. magister*, thereby increasing visibility. Placing the tag at the epimeral suture line is assumed to assure a high retention rate when the old shell is discarded during a moult. To test this assumption, tag retention was estimated by double tagging 850 sublegal-sized males as previously described, except the second tag was inserted through the left posterior epimeral suture line.

Most recoveries were obtained from fishermen and research traps. Four fishermen recorded the date, location, and tag number of all tagged crabs they recovered on special recovery forms. Most other fishermen generally ignored recoveries of sublegal-sized males, but retained tags from legal-sized males. From April until August in 1985 and 1986 we interviewed most fishermen at least biweekly, and at other times, monthly.

TABLE 1. Tag retention by double tagged male *C. magister*. For males that did not moult the mean and median days-at-large were 83 and 69, respectively.

For males that did not moult	
Recoveries with two tags	59
Recoveries with one tag	4
Proportion retained (122/126)	0.968
For males that moulted	
Recoveries with two tags	64
Recoveries with one tag	1
Proportion retained (129/130)	0.992

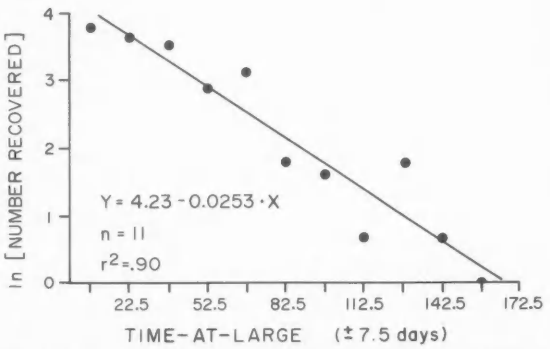

FIG. 2. Linear regression of recoveries over time for tagged male *C. magister* released and recovered as legal-sized crabs, mostly in spring 1986.

Results

Fishing and Natural Mortalities

From Fig. 1 we estimated the annual instantaneous rate of disappearance of sublegal-sized males as the negative slope of the linear relationship times 365 d (≈3.5, 95% confidence interval (CI) is 2.9–4.1) (Gulland 1983, p. 110, equation (4.33)). Note that the quadratic model in Fig. 1 is equally plausible. It suggests the rate of disappearance of tagged

TABLE 2. Summary of survivorship to legal size for male *C. magister* which were tagged when sublegal size, and recovered when legal size.

Premoult carapace width (mm)	Number tagged	Recoveries		Percent surviving to legal size[a]	Mean days at large[b]	Instantaneous annual mortality
		n	(%)			
125–130	168	20	11.9	32.1	165	2.87
130–135	310	50	16.1	24.0	196	2.96
135–140	366	52	14.2	19.2	227	2.91
140–145	499	35	7.0	9.5	258	3.56
145–150	1027	28	2.7	3.7	289	4.37
150–155	1219	25	2.1	2.8	320	4.27

[a]Calculated by multiplying the percent recovered in each 5-mm CW interval by 1.15 to compensate for the compliance (C) estimate of 0.87. The percent recovered in intervals, 125–130- and 130–135-mm CW was further multiplied by 2.0 and 1.1, respectively, because only 50 and 90% of crabs this size are expected to attain legal size with their next moult (Smith and Jamieson 1989b).

[b]Estimated from Fig. 3

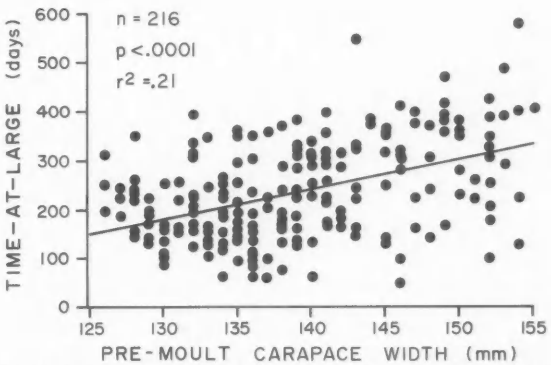

FIG. 3. Linear regression of time-at-large on premoult carapace width for male *C. magister* tagged and released when sublegal size and recovered when legal size.

sublegal-sized males increases with time-at-large. The rate of tag loss is low (Table 1), and observations over several months of tank-held tagged and untagged crabs did not suggest differential mortality. We also suspect that mortality is not seriously confounded with movement from the study area (B. D. Smith, unpubl. data); therefore, the aforementioned rate mainly estimates the combination of M (annual instantaneous rate of natural mortality) and the instantaneous rate of moulting into legal size. Thus $M = 3.5$ can be considered a maximum estimate.

The short time-at-large for the 182 recoveries of the 341 legal-sized males released indicates a high exploitation rate. The total annual instantaneous rate of disappearance of legal-sized males (Z) is the negative slope of the linear relationship in Fig. 2 times 365 d (= 9.2, 95% CI is 7.2–11.2) (Gulland 1983). A provisional and minimum estimate of the annual instantaneous rate of fishing mortality (F) is thus 4.9 (= (0.534)(9.2)), since 0.534 (182/341) is a minimum estimate of the proportion of tagged legal-sized males reported upon capture. We will refer to this proportion as compliance (C). Consequently, a maximum annual instantaneous rate of 4.3 (9.2–4.9) accounts for a lack of recoveries for all other reasons. Excluding movement from the study area, tag loss, and tagging-induced mortality, whose importance we have diminished, other reasons for these tags not being recovered are natural mortality and a lack of compliance in reporting recovered tagged crabs.

TABLE 3. Percent of male *C. magister* tagged when soft-shelled, which were hard-shelled when recovered. A crab was considered hard-shelled if the exoskeleton of its legs could resist moderate pressure applied by the thumb and index finger. The results are reported for 30-d intervals of time-at-large. The carapace widths of recovered males were approximately normally distributed ($\mu = 153$ mm, $\sigma = 6$ mm) and ranged from 135–173 mm.

Time-at-large (d)	Sample size	Percent hard-shelled
1–30	31	32.3(σ = 8.4)
31–60	20	60.0(σ = 11.0)
61–90	23	91.3(σ = 5.9)
>90	56	100.0

Mortality estimates for males expected to attain legal size with their next moult (Table 2), were hindered by uncertainty in the (minimum) compliance estimate of 0.534. However, our estimate of compliance can be revised as follows. For carapace width intervals 145–150 and 150–155 mm (Table 2), which include those males closest to legal size and mainly within the $\mu = 156$-mm CW instar (see Fig. 5), M can be provisionally estimated as the negative log of the proportion recovered, corrected for time-at-large (equation (1)). Time-at-large was estimated from the regression in Fig. 3, which also (1) indicated a trend toward a longer intermoult period with increasing carapace width, and (2) provided a minimum estimate of the length of the intermoult period.

(1) $M = -\ln(53/2246)(365/305) = 4.48.$

By incorporating a correction for compliance (C), M becomes:

(2) $M = 4.48 + \ln(C).$

From Fig. 2:

(3) $Z = 9.2 \pm 2.0,$

therefore

(4) $F = 0.534Z/C$

and

(5) $M = Z - (0.534Z/C).$

If one assumes estimates for each of M and C are the same for both analyses, then an estimate of C can be obtained by solving equations (2) and (5) simultaneously for a single estimate of M. Within the 95% confidence limits of Z (7.2 − 11.2), no corresponding estimate of M was obtainable for $Z < 9.6$ because C cannot exceed 1.0. For $Z = 11.2$, $C = 0.87$, and $M = 4.3$. The range of M for C ranging from 0.87–1.00 is 4.3–4.5, and the range for F is 5.1–6.9. We closely monitored this fishery and believe $C = 0.87$ is plausible. Table 2 reports estimates of M assuming $C = 0.87$. Our results suggest size-dependent mortality, with larger crabs having lower survivorship.

The estimate of $M = 4.3$–4.5 through a moult (from Table 2) for males 145–155-mm CW is higher than the maximum estimate of $M = 3.5$, based on recoveries of sublegal-sized males that did not moult (Fig. 1). An explanation for this discrepancy is higher mortality for males during, or while soft-shelled following, the moult to legal size. If so, then the assumption of equal M's above does not strictly hold, thereby resulting in

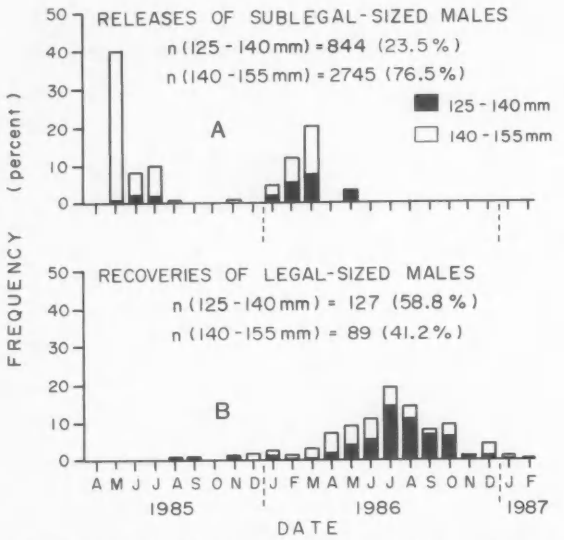
RELEASES OF SUBLEGAL-SIZED MALES
n (125 - 140 mm) = 844 (23.5 %)
n (140 - 155 mm) = 2745 (76.5 %)
125 - 140 mm
140 - 155 mm
A
RECOVERIES OF LEGAL-SIZED MALES
n (125 - 140 mm) = 127 (58.8 %)
n (140 - 155 mm) = 89 (41.2 %)
B
FREQUENCY (percent)
A M J J A S O N D J F M A M J J A S O N D J F
1985
1986
1987
DATE

FIG. 4. Releases (when sublegal size) and recoveries (following the moult to legal size) of male *C. magister*. (A) Temporal distribution of releases. (B) Temporal distribution of recoveries.

an underestimate of F and an overestimate of M. Our study also does not permit distinction in Fig. 1 between the disappearance of sublegal-sized males due to moulting to legal size and disappearance due to mortality; nor in Table 2 between pre- and immediately postmoult mortality.

It takes ≈3 mo for legal-sized males to become hard-shelled following a moult (Table 3), and because of the intensity of the fishery near Tofino, only a small proportion of males survive to become hard-shelled. For our estimates of $F = 5.1$–6.9 only 18–28% of legal-sized males would survive 3 mo. In commercial samples taken during the peak moulting period (spring–summer) ≈50% of legal-sized males were soft-shelled. The trapping and handling of soft-shelled sublegal- and legal-sized males is likely an important contributor to postmoult mortality.

Moulting Season

From recoveries of males 125–155-mm CW (sublegal size) when tagged and legal size when recovered, and in consideration of the high exploitation rate ($F = 5.1$–6.9), Fig. 4b profiles the moulting season for males attaining legal size. Moulting appeared to occur all year, but mostly in summer. Corroborating Table 2, Fig. 4 also indicates that survivorship to the next instar decreases with size, with a smaller percent of crabs 140–155-mm CW attaining legal size than those 125–140-mm CW. This appears not to result from insufficient intermoult time since tagged crabs were monitored for 400–600 d, and nearly all moulting was observed in <400 days-at-large. The annual instantaneous rate of disappearance of sublegal-sized males of 3.5 (from Fig. 1) suggests 400 d is sufficient time for males to either moult or die, since <3% of these crabs were present after 400 days-at-large, and we discounted movement from the study area as an important source of disappearance.

Commercial Exploitation of Males

We define percent exploitation as the percent of legal-sized males missing from a SFD which would otherwise be composed

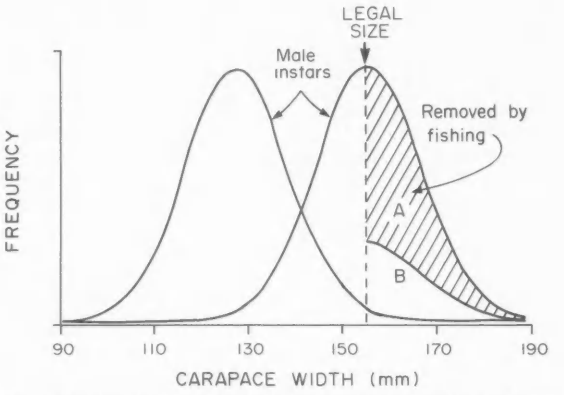

FIG. 5. Diagrammatic explanation of the effect of fishing on the apparent instar composition of a SFD. Percent exploitation of male *C. magister* in the $\mu = 156$-mm CW ($\sigma = 13$-mm CW) instar, $100A/(A+B)$, was determined by SFA. The $\mu = 129$-mm CW ($\sigma = 12$-mm CW) instar is also shown.

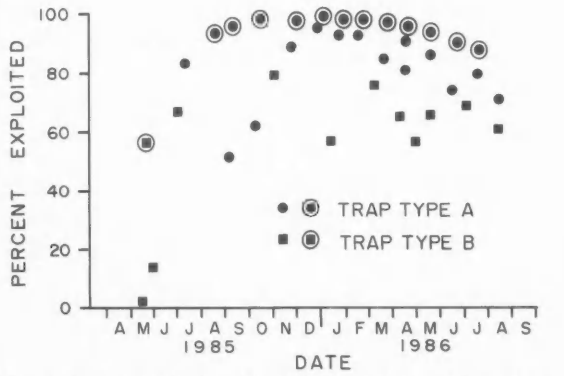

FIG. 6. Percent exploitation of legal-sized male *C. magister* as determined by SFA of trap samples. Encircled data points are for upper Lemmens Inlet, while the remainder are for the rest of the study area.

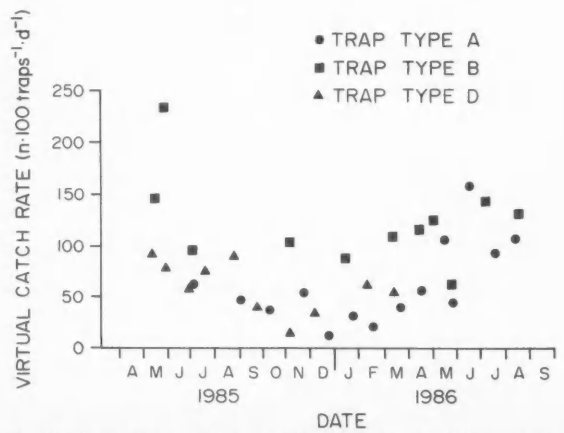

FIG. 7. Virtual catch rates of legal-sized male *C. magister* over time (excluding data from upper Lemmens Inlet).

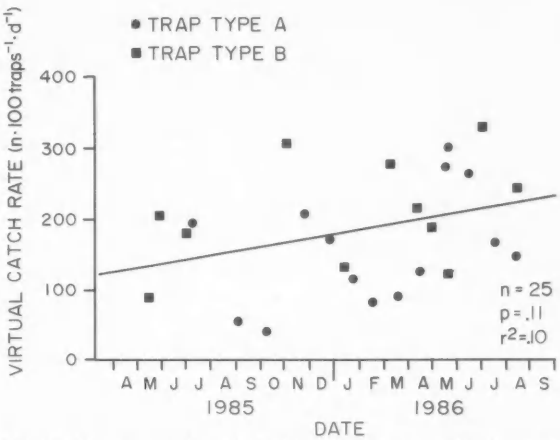

FIG. 8. Linear regression of virtual catch rates over time for male *C. magister* 145–155-mm CW (excluding data from upper Lemmens Inlet).

of a mixture of normal instars. Since there is little overlap in the legal size range between the adjacent $\mu = 129$ and $\mu = 156$-mm CW instars (Fig. 5), percent exploitation was estimated using a SFA which estimated the percent of legal-sized males missing from only the $\mu = 156$-mm CW instar. The influence of the next larger $\mu = 185$-mm CW instar on the SFAs was considered insignificant because low survivorship precluded most males from attaining this instar. Despite the $\mu = 129$ instar being quite distinct from the $\mu = 156$-mm CW instar, we further reduced its influence in the SFAs by performing the SFAs only on that portion of a SFD >145-mm CW. About 58% of the $\mu = 156$-mm CW ($\sigma = 13$-mm CW) instar is composed males greater than legal size. Since males are continually moulting into the $\mu = 156$-mm instar, the estimate of percent exploitation results from the difference between the rate of recruitment of legal-sized males to this instar and their subsequent rate of exploitation.

Before performing a SFA measuring percent exploitation, SFDs were standardized to minimize bias introduced by different soak times (Smith and Jamieson 1989a). The standardization model estimated the 'virtual catch rates' for each 5-mm CW interval which, after the appropriate soak time, minimized the discrepancy between the predicted and observed SFD for the commercial sample. As in Smith and Jamieson (1989a), the SIMPLEX algorithm of Mittertreiner and Schnute (1985) was used to obtain parameter estimates by minimizing the separation statistic A of Schnute and Fournier (1980). We used the parameter estimates for the agonistic-interactions and bait-effectiveness equations obtained from the experiments near Indian Island, because this site was more typical of commercially fished areas.

The percent of legal-sized male *C. magister* taken by the fishery between April 1985 and August 1986 increased rapidly in spring 1985 and remained at 60–90% (Fig. 6). In upper Lemmens Inlet exploitation was near 100%. Virtual catch rates of legal-sized males were highest during spring and summer and lowest in winter (Fig. 7). Because of the intensity of the fishery ($F = 5.1$–6.9), Fig. 7 roughly profiles the seasonal moulting pattern for males attaining legal size, as was also interpreted from Fig. 4.

The rapid increase in exploitation of legal-sized males in spring 1985 suggested that fishermen increased their effort in response to a strong recruitment of legal-sized males. Corroborating our suggestion of an increase in recruitment of legal-sized males, the virtual catch rates for sublegal-sized males 145–155-mm CW approximately doubled in the 18 mo following spring 1985 (Fig. 8). The recruitment rate of sublegal-sized males over this period was probably much greater than suggested by an increase in virtual catch rate, because Fig. 8 considers only net population growth, and we estimated natural mortality to be high.

Discussion

The high fishing mortality ($F = 5.1$–6.9) estimated by mark–recovery methodology was corroborated by analysis of population size frequency structure which indicated a high percent exploitation of legal-sized males. High fishing mortality rates have previously been measured for *C. magister* in northern California. Jow (1965) estimated $F = 7.9$, based on recovery of tagged legal-sized males during a 6 mo fishing season. Using catch-per-unit-effort data, Gotshall (1978a) estimated F to range from 1.2–7.0, depending on the year. Methot and Botsford (1982) similarly estimated F to range from 0.8–3.2 from 1951–77.

Such intense fishing means a large proportion of soft-shelled legal-sized males are caught. Short-term closures to allow crabs to harden would seem to have little benefit since hard-shelled crabs would be rapidly exploited, and the fishery would revert to being sustained by recently moulted crabs. Hard-shelled crabs are preferred by most fishermen because they command a higher price for their greater meat yield. However, new markets for soft-shelled males have resulted in many fishermen reluctantly retaining them in order to remain competitive. Soft-shelled crabs probably experience more trapping and handling mortality than do hard-shelled crabs, and might benefit from fishery closures, but if our estimate of M is reasonable for crabs near legal size then there remains an argument for continuous fishing.

Natural mortality is high, with some of the variation in our estimate of M (2.9–4.5) resulting from differences in crab size and molt stage. Variation in M is a reasonable expectation, and Gotshall (1978b), using catch-per-unit-effort data, estimated M to range from 0.88–2.50 in northern California. We observed increasing natural mortality rates with increased size (Table 2). Hankin et al. (1985) observed the same pattern for female *C. magister*, and attributed this partly to senescence concomitant with shell deterioration. We also observed shell deterioration and a loss of vigor among prerecruit males as the time since their last moult increased. Figure 3 indicates that the intermoult period tends to increase with increasing carapace width, thereby extending the time over which shell deterioration might occur. Consistent with the concept of senescence, the quadratic relationship in Fig. 1 suggests that mortality rate might increase as intermoult time increases. An increasing natural mortality rate with increasing size has been observed for other crab species. For example, Hill (1975) reported an increase in the mortality rate of the portunid crab, *S. serrata*, from its second to third year of life.

The high mortality rates obtained in our study might be related to unusually high *C. magister* abundance in 1986. The 265 t landed in SA 24 in 1986 was the third highest total in the history of the fishery, and more than double the mean annual tonnage landed in the previous 10 yr ($\mu = 131$ t, $\sigma = 26$ t). How-

ever, SFA on standardized trap samples from the lightly fished Holberg Inlet (northern Vancouver Island) fishery also indicated low survivorship from the $\mu = 156$ to the $\mu = 185$-mm male instar (Smith 1988).

There is no evidence that disease is a factor in *C. magister* mortality near Tofino (S. Bower, Pacific Biological Station, Nanaimo, B.C., pers. comm.), but predation is a possibility. The giant Pacific octopus, *Octopus dofleini*, an important predator of *C. magister* (High 1976b; Hartwick et al. 1978), is abundant in this vicinity. *Octopus dofleini* were occasionally caught in crab traps during this study, and High (1976a) observed *O. dofleini* predation on *C. magister* during trap escapement experiments.

The mortality rate estimates for males obtained in this study might have implications for models proposed to explain the cyclical nature of *C. magister* landings in California (see McKelvey et al. 1980; Botsford 1984, 1986; Methot 1986). These models have presumed mortality rates much lower ($M = 0.15$–0.90 for sublegal-sized males) than those presented here. If our mortality estimates are applicable to populations where cycles in abundance are pronounced, then these models might need revision. Our high mortality estimates also question the appropriateness of the current minimum legal size limit of 165 mm spine-to-spine carapace width for achieving optimal levels of yield- and eggs-per-recruit. Our future work on Dungeness crab will address yield- and eggs-per-recruit questions.

Acknowledgments

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Analysis of Otolith Microstructure to Determine Growth Histories in Larval Cohorts of a Tropical Herring (*Herklotsichthys castelnaui*)[1]

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Thorrold, S. R., and D. McB. Williams. 1989. Analysis of otolith microstructure to determine growth histories in larval cohorts of a tropical herring (*Herklotsichthys castelnaui*). Can. J. Fish. Aquat. Sci. 46: 1615–1624.

Otolith microstructure was used to characterize growth in five cohorts of larval *Herklotsichthys castelnaui* from Townsville, north eastern tropical Australia in spring/summer of 1987. Ontogenetic development of larval *H. castelnaui* is described, and is correlated with changes in otolith microstructure. Development of fin rays coincided with a period of rapid otolith and somatic growth. Otolith increment width and water temperature series were modelled for each cohort using time series analysis. Cross-correlation functions showed no detectable dependencies between increment widths and temperature. Length-at-age relationships were significantly different among cohorts. Repeated-measures analysis of variance was used to establish differences in increment spacing among cohorts. Measurement of otolith radii allowed back-calculation of absolute growth rates of cohorts over the first 30 d of larval life. Significant differences in growth trajectories were detected among cohorts. Data presented here suggest that growth may vary among cohorts separated by as little as 2 wk, and that these differences are detectable by otolith increment analysis.

La microstructure des otolithes a servi à caractériser la croissance chez cinq cohortes de larves de *Herklotsichthys castelnaui* de Townsville, dans le nord-est de l'Australie tropicale, pendant le printemps et l'été 1987. Nous décrivons le développement ontogénique des larves de *H. castelnaui*, que nous corrélons avec les changements dans la microstructure des otolithes. Le développement des rayons de nageoires correspondait à une période de croissance rapide des otolithes et du corps. La largeur de l'anneau de croissance des otolithes et les séries des températures de l'eau ont été modélisées pour chaque cohorte par analyse de séries choronologiques. Les fonctions de corrélation croisée n'ont révélé aucune dépendance détectable entre la largeur des anneaux de croissance et la température. Les relations longueur–âge étaient nettement différentes d'une cohorte à l'autre. L'analyse de variance des mesures répétées a servi à établir des différences entre les cohortes dans l'espacement des anneaux de croissance. La mesure du rayon des otolithes a permis de calculer rétrospectivement les taux de croissance absolue des cohortes pendant les 30 premiers jours de vie larvaire. Des différences notables dans les schémas de croissance sont apparues entre les cohortes. Les données présentées ici indiquent que la croissance pourrait varier entre des cohortes séparées de 2 sem seulement, et que ces différences sont détectables par analyse de la croissance des ithes.

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The potential for growth dynamics to influence larval fish survivorship and subsequent recruitment has been realized since the beginning of the century (Hjort 1914). However, this hypothesis has rarely been tested, owing to the difficulties of obtaining unbiased growth estimates (Crecco et al. 1983). Early attempts to correlate growth with survivorship were unsuccessful (May 1974; Dahlberg 1979), as growth rates estimated from length-frequency curves are often biased by age and cohort-specific changes in larval growth rates (Lough et al. 1982). These difficulties are compounded when critical life-history events occur on short temporal scales of hours or days (Fortier and Leggett 1985), linked to plankton patchiness on spatial scales of 1–10 m (Lasker 1981).

Otolith analysis has considerable potential to provide detailed information on growth dynamics of larval fishes (Campana and Neilson 1985). Aging individual larvae by counting daily growth increments allows a direct measure of length-at-age. This information can be used to calculate growth curves (e.g. Struhsaker and Uchiyama 1976; Methot and Kramer 1979) and to estimate temporal distributions of birthdates (e.g. Methot 1983; Graham and Townsend 1985). Data may then be combined to compare both spatial (e.g. Methot 1983; Thomas 1986) and temporal (e.g. Jones 1985; Leak and Houde 1987) variability in growth rates.

Otolith microstructure has been shown to be sensitive to both environmental changes, and ontogenetic transitions, during the early life of fishes. Several studies have documented the response of otolith growth to changes in temperature (e.g. Brothers 1981; Campana 1984; Mosegaard et al. 1988) and food levels (Marshall and Parker 1982; Neilson and Geen 1982; Rice et al. 1985). Otolith microstructure may also record eco-morphological transitions in the early life history of some fishes (Brothers and McFarland 1981; Nishimura and Yamada 1984).

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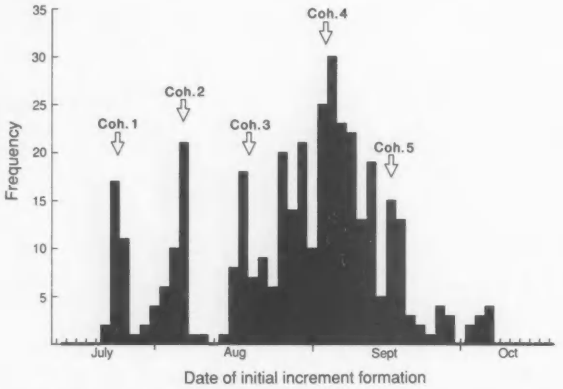

FIG. 1. Back-calculated dates of initial increment formation in otoliths of *Herklotsichthys castelnaui*. Arrows show timing of quarter moon phases — individuals were assigned to a particular cohort if date of initial increment formation was within 2 d either side of a quarter moon phase.

These transitions may indicate changes in growth trajectories (Neilson et al. 1985; Kingsford and Milicich 1987), or discrete periods of reduced growth (Victor 1986).

It may also be possible to reconstruct individual growth histories by quantification of otolith increment widths. A close relationship between somatic and otolith growth at a daily level implies that the width of any growth increment is a measure of instantaneous growth (see Campana and Neilson 1985 for review). Volk et al. (1984) reported a direct relationship between mean daily otolith increment width and fish growth, and good correlations have been demonstrated between the width of daily rings and increase in length (Taubert and Coble 1977) and weight (Wilson and Larkin 1982). Assuming that otolith and somatic growth are related, examination of incremental width series would allow estimates of both size-at-age and instantaneous growth rates over short time periods.

The ability to determine individual growth rates is a major advantage of otolith analysis in larval fish studies. Although this technique has been used to detect growth differences over periods of months (e.g. Jones 1985; Leak and Houde 1987), it has been used only infrequently to examine growth rates in field situations on smaller temporal scales (Crecco et al. 1983; Penny and Evans 1985; Rice et al. 1987). In this paper, we document differences in both growth and otolith microstructure in larval *Herklotsichthys castelnaui* cohorts. *Herklotsichthys castelnaui* is a coastal pelagic clupeid found along the eastern seaboard of Australia (Whitehead 1985), inhabiting estuaries and inlets (Robertson and Duke 1987). Daily periodicity of otolith increment deposition has been validated for this species (Thorrold 1988). We posed several specific questions. Is otolith microstructure related to temperature, growth, or ontogenetic development in *H. castelnaui*? If so, do these relationships vary among cohorts? The above information may then be integrated to form detailed growth histories of a series of larval cohorts.

Materials and Methods

Sample Collections and Cohort Identification

Larvae were collected from Breakwater Marina, Townsville, Australia during August to November 1987 (see Thorrold, 1988 for description of study area and capture methods). Ontogenetic development of *Herklotsichthys castelnaui* was described from a size series collected from the study site. General terminology of the larval descriptions follows that of Fahay (1983). A semilunar spawning periodicity within the study area has been documented (Thorrold 1988). To ensure precise allocation of larvae to a cohort, larvae were assigned to one of five cohorts if birthdates were within 2 d either side of a first- or last-quarter moon phase (Fig. 1). Date of initial increment formation was used in this study as reared larvae were not available to determine the relationship between the time of initial increment formation and spawning date. Given high water temperatures and fast development rates, the two are unlikely to differ by more than 2 d. The five cohorts determined thus had birthdates separated by 2 wk. Details of numbers of larvae examined for otolith information are given in Table 1.

TABLE 1. Summary of the number of *Herklotsichthys castelnaui* larvae examined in each cohort for aging and measurement of otolith widths.

	Aging	Increment widths
Cohort 1	28	14
Cohort 2	32	15
Cohort 3	31	18
Cohort 4	31	28
Cohort 5	30	12
Total	152	86

Daily water temperatures during the sampling period were calculated from air temperature records collected at 6-h intervals at Cape Cleveland, Townsville (see Fig. 1; Thorrold 1988). A linear relationship between water temperature (T_s) and air temperature (T_a) at 0900 has been documented for Cleveland Bay (Walker 1981), and has the equation

$$(1) \quad T_s = 0.8T_a + 0.6$$

and was used to calculate daily water temperatures over the sampling period.

Otolith Analysis

Length-at-age of larval *H. castelnaui* was determined by counting daily growth increments on otoliths. Otolith analysis was restricted to sagittae. Otoliths were mounted in immersion oil for microscopic examination. Validation of daily periodicity of increment formation and the technique of otolith analysis are described in Thorrold (1988). Analysis of covariance (ANCOVA) was then used to detect differences in length–age relationships among cohorts.

Widths of otolith increments were measured in a random sample of larvae from each cohort (Table 1). Each increment in all of these otoliths was measured. All measurements of otoliths were made at 1000× magnification using a polarized transmitted light source, along the longest radius of the sagitta. An Ikegami high resolution camera was fitted to the microscope, which was in turn interfaced with a Commodore Amiga personal computer. Increment widths were calculated using the computer mouse to position a cursor on the video image. An incremental width was taken to be the distance between the dark discontinuous zones (Mugiya et al. 1981), constituting growth of the otolith on that day (Fig. 2).

Measurements of increment widths were also used to estimate individual growth histories. Given a logarithmic relationship between otolith radius and standard length:

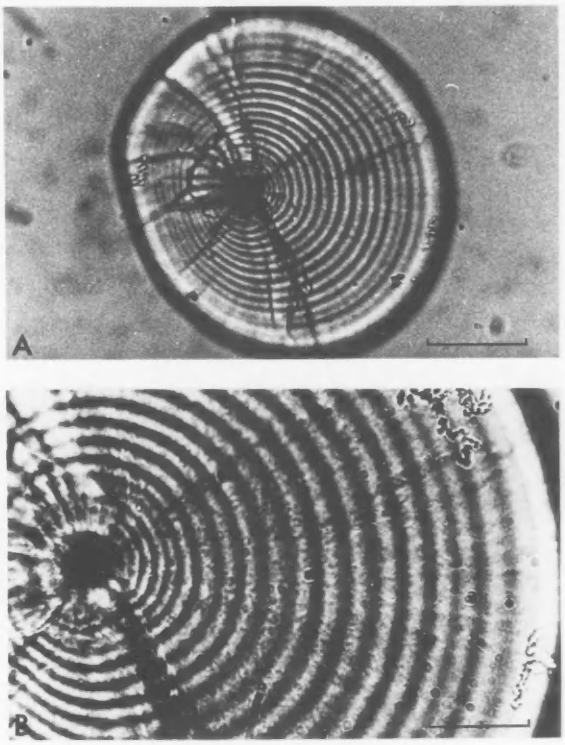

FIG. 2. Photomicrograph of a sagitta from a *Herklotsichthys castelnaui* larva with 22 growth increments: (A) at 250× magnification (scale bar = 60 μm) and (B) at 1000× magnification (scale bar = 25 μm).

$$(2)\quad SL = a \cdot \log_e OR + b$$

where SL = standard length of a larva at time of capture, OR = radius of sagittae and a and b are constants estimated by linear regression of $\log_e$OR on SL. The length SL_i of a larva at an intermediate age i was back-calculated using the equation determined by Thorrold (1988).

$$(3)\quad SL_i = 5.61 \cdot \log_e OR_i - 10.56$$

and the mean daily growth rate g_i in a 3-d age interval ending at age i from the formula

$$(4)\quad g_i = \frac{(SL_i - SL_{i-3})}{3}.$$

Individual growth rates were averaged over 3-d intervals, beginning at day 3 and ending at day 30. Ages at which analysis began and finished were chosen to avoid extrapolation beyond the available data. Growth rates were averaged over 3 d to allow for some delayed response of otolith growth to changes in fish growth (see discussion).

Statistical Analyses

The relationship between water temperature and increment width series were analysed by means of time series analysis in the time domain (Box and Jenkins 1976). Both temperature and increment width series were modelled employing an autoregressive-integrated moving average (ARIMA) model (see Gutierrez and Morales-Nin 1986 for a detailed discussion of this approach). These are stochastic models, based on the properties of stationary time series. Trends in temperature and otolith widths were removed by differencing both series. Model identification was based on examination of the autocorrelation and partial autocorrelation functions of the series. Cross-correlation functions of the two models were then used to identify any relationship between increment widths and water temperature. All time series analyses were carried out using the MINITAB statistics program.

The increment width data were analysed for differences among cohorts using repeated-measures ANOVA (Winer 1971). The Greenhouse–Geisser adjustment factor was used when calculating significance of within subject (i.e. individual larvae) effects to account for the correlative nature of repeated measurements on the same otolith. Further interpretation of the results from this analysis was conducted using a polynomial transformation of time (SAS 1985). Polynomial contrasts provide estimates of the significance of linear, quadratic, cubic, etc. trends for time, and further test for differences in each of these trends among cohorts.

ANOVA and Student–Newman–Keuls multiple comparisons tests were used to examine whether individual larval growth rates differed significantly among cohorts. All statistical tests were performed separately on the growth data from the eight age groups to evaluate the extent to which growth differences among cohorts were related to age. Data were tested for normality of residuals and homogeneity of variances using residual analysis (Winer 1971).

Results

Larval Development

Dorsal fin rays began to form in larval *H. castelnaui* at 6.5 mm SL (Fig. 3), with a full complement present by 10 mm SL. Anal fin development commenced at 8 mm SL, rays were developing at 8.5 mm SL, and a full fin ray complement was obtained by 12 mm SL. The caudal fin developed coincidently with the dorsal fin: principal caudal rays were present at 7.5 mm SL and the full complement was reached by 9 mm SL. Flexion of the notocord commenced at 7.5 mm SL and was complete by 10.5 mm SL. Pelvic and pectoral fin development was initiated somewhat later; a full complement of these fin rays was not reached until around 17 mm SL. Larval *H. castelnaui* thus had an adult fin ray complement of the major locomotory fins (dorsal, anal, and caudal) by 12 mm SL, corresponding to an age of between 8 and 18 d.

Temperature and Otolith Increment Series

Water temperature generally increased throughout the study (Fig. 4), from a low of 22°C (cohort 1) to a high of 30°C (cohort 5). Spacings of otoliths changed with distance from the primordium (Fig. 4). Increments were narrowest for the first 2 to 8 d, followed by a period of rapid increase in increment width for 10–20 d. Spacing of increments in all individuals varied from 4 to 7 μm between days during the latter stage.

Temperature and increment width series were analysed separately for each cohort. The appropriate model for each series was identified by examination of the autocorrelation functions of the differenced series. Parameters for the temperature series were estimated, and the degree of fit of the parameters checked using a t-distribution (Table 2). The fitted models were then

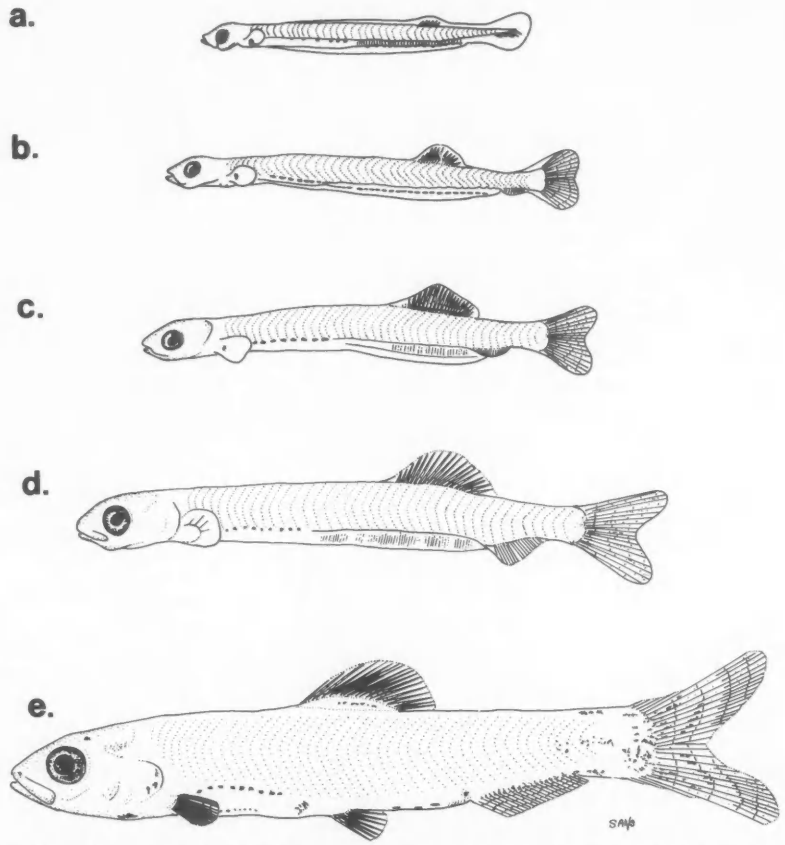

FIG. 3. Developmental series of *Herklotsichthys castelnaui* larvae: (a) 6.5 mm SL; (b) 8.6 mm SL; (c) 9.8 mm SL; (d) 12.5 mm SL; (e) 20.8 mm SL.

verified by examination of the autocorrelation and partial autocorrelation functions. All increment width series were "random walk models," and hence no parameters were estimated for these series.

Cross correlation functions between water temperature and increment widths were estimated for each cohort (Fig. 5). No significant correlation was found when either water temperature was moved over increment widths, or increment widths were moved over water temperature.

Length–Age Relationships and Individual Fish Growth

Standard length of larval *H. castelnaui* were $\log_e$ transformed due to the curvilinear nature of length–age relationship (Thorrold 1988). To ensure even age structures for analysis, only larvae older than 10 d were considered. Slopes of the lines (Fig. 6) differed significantly (ANCOVA, $p<0.05$). Cohort 2 had the highest slope, followed by cohorts 1, 4, 5, and 3, which were similar. If cohort 2 was eliminated from the analysis, slopes were no longer significantly different (ANCOVA, $p>0.1$). Intercepts were, however, significantly different (ANCOVA, $p<0.05$; 4>3>1>5). This suggested that larvae of a given age differed in size, although no differences were detected in growth rates of the cohorts over the period considered.

Repeated measures ANOVA detected significant differences in increment widths over time and between cohorts (Table 3). A significant time–cohort interaction term suggested further that the relationship among cohorts changed over time. Polynomial contrasts of time found significant linear and quadratic trends only (Table 3). These trends were significantly different among cohorts. Although the significant linear contrast has little interpretive value, the highly significant cohort effect for the quadratic trend with time suggests differences in increment width curves among cohorts. Cohorts 1 and 2 had longer periods of narrow increment spacing at the onset of ring deposition than cohorts 3, 4, and 5. The plateau in increment widths was therefore reached quicker (after 8–10 d) in the last three groups than in cohorts 1 and 2 (after 18–22 d). Cohort 5 differed from cohorts 3 and 4 in the height reached by the plateau (4 μm in cohort 5; 5–5.5 μm in cohorts 3 and 4).

The relationship between standard length and otolith radius was used to back-calculate instantaneous growth rates averaged over 3 d for the first 30 d of larval life (Fig. 7). Growth rates declined from 1 $mm \cdot d^{-1}$ between 3–6 d to 0.2–0.3 $mm \cdot d^{-1}$ between 27–30 d. Growth trajectories also differed between cohorts (Table 4). Cohorts 3 and 4 had significantly higher growth rates initially than the three other cohorts. This changed, however, with time; after 12 d, cohort 1 grew faster than the other cohorts, and cohort 2 had higher growth rates after 21 d.

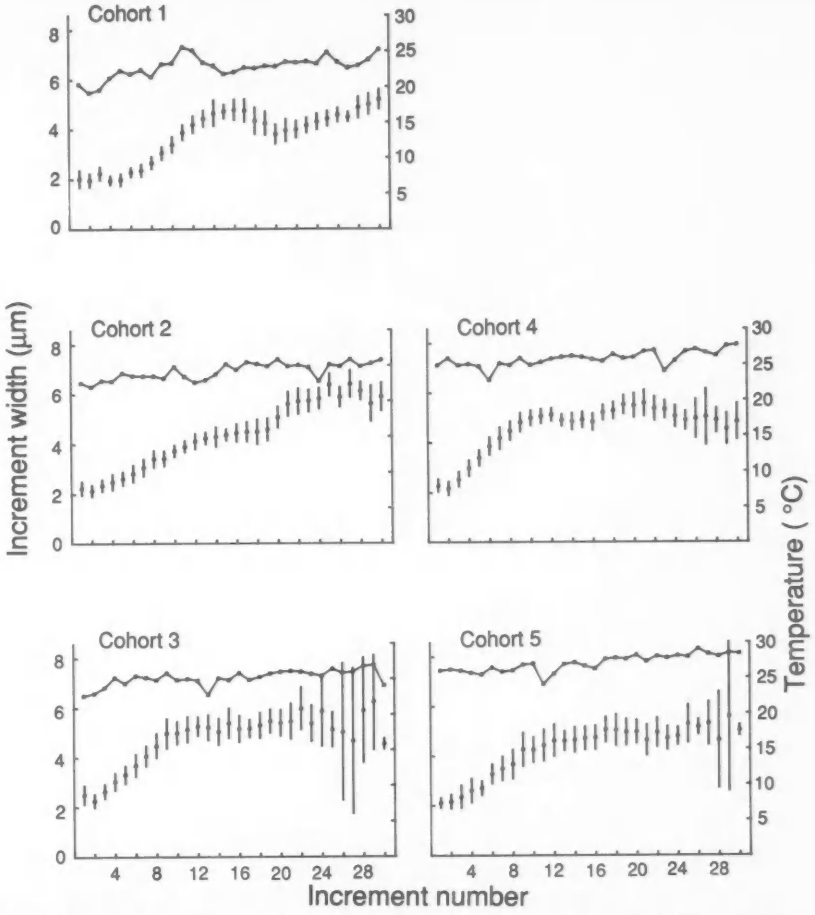

FIG. 4. Relationships between the number of daily growth increments and mean (±95% confidence intervals) increment width in five cohorts of *Herklotsichthys castelnaui* larvae. Inferred daily water temperature for each cohort is also shown (continuous line).

TABLE 2. Time series models identified for each temperature series, estimated parameter values, standard errors of the parameter estimates, and the degree of fit (*$p<0.05$; **$p<0.01$; ***$p<0.001$).

	Adjusted model	Parameter	SE	*t*-value
Cohort 1	ARIMA (1,1,1)	$\phi_1 = 0.737$	0.063	2.13*
		$\phi_1 = 0.876$	0.046	3.46**
Cohort 2	ARIMA (0,1,1)	$\phi_1 = 0.527$	0.030	3.22**
Cohort 3	ARIMA (0,1,1)	$\phi_1 = 0.534$	0.032	3.09**
Cohort 4	ARIMA (0,1,1)	$\phi_1 = 0.687$	0.028	4.48***
Cohort 5	ARIMA (0,1,1)	$\phi_1 = 0.607$	0.027	4.03***

Discussion

Otolith spacings in this study were assessed using light microscopy. It has become apparent, however, that limitations in the resolving power of light microscopes may complicate interpretation of otolith microstructure (Campana 1984). A lack of resolution may be responsible for the failure of several workers to find daily rings on otoliths (Jones and Brothers 1987); an inability to distinguish daily increments invalidates both length-at-age data and attempts to measure increment spacings. Results presented here can be used to examine the likelihood of resolution problems in *H. castelnaui* otoliths. The smallest increment measured in this study was 0.95 μm. Most increments were, however, greater than 2 μm in width. The functional resolution of light microscopy is around 0.25 μm, and almost all increments were above the width (≈1 μm) at which a lack of resolution may make individual increments indiscernable (Campana et al. 1987). The pattern of otolith spacings further argue that resolution was not a complicating factor in this study. An allometric relationship between otolith growth and standard length implies that a lack of resolution is most likely to be encountered near the primordium. Increment widths did not appear to increase near primordia, indicating they were not aggregates of poorly resolved increments.

No dependencies were detected between water temperature and intra-cohort increment width series. This is in contradiction to a number of studies documenting the influence of temperature on otolith growth (e.g. Neilson and Geen 1982; Gutierrez and Morales-Nin 1986). Temperature may, however, have been a causal factor in differences among cohorts. Temperature dif-

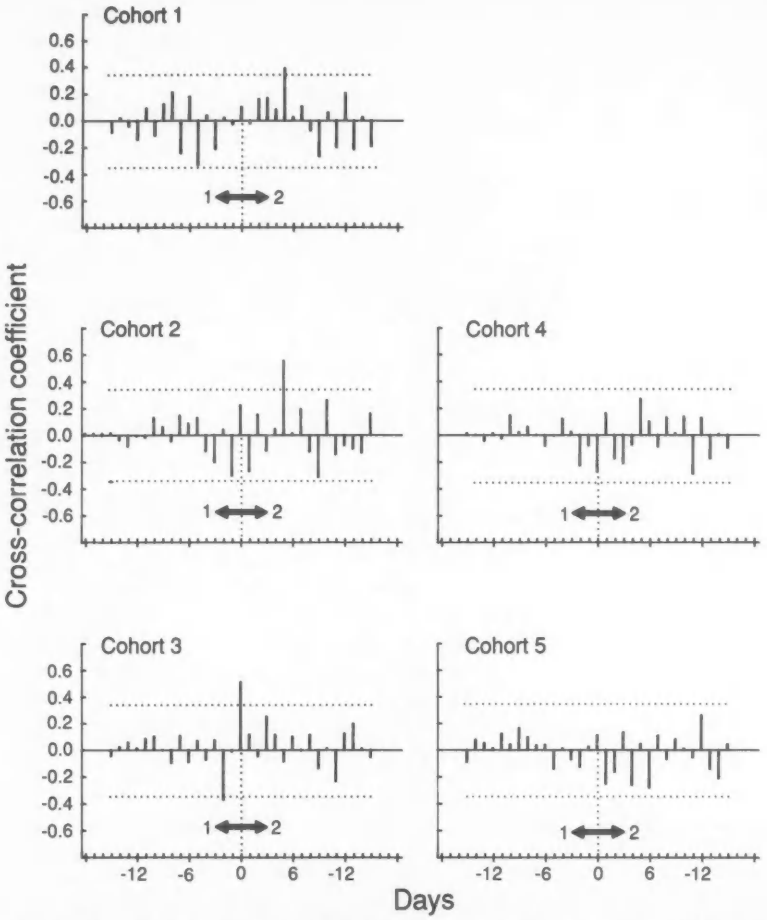

FIG. 5. Estimated cross-correlation coefficients between water temperature and otolith increment width series: (1) increment width series moved over water temperature series and (2) water temperature series moved over increment width series. Dotted lines represent two standard error limits.

ferences among cohorts were greater than the variability experienced within cohorts. Temperature may also affect somatic and otolith growth in young larvae more than older ones (Savoy and Crecco 1987). Lower water temperatures during the initial stages of cohort 1 and 2 may have led to the observed differences in increment width series among cohorts. The existence of an optimum temperature for growth in *H. castelnaui* may explain (in an admittedly ad hoc manner) the reduced increment widths in cohort 5, despite the presence of high water temperatures. Such optima have been reported for other species (e.g. Boehlert 1981).

Prey availability may also have had a considerable impact on differences in increment widths among cohorts (e.g. Rice et al. 1985; Reckmann and Rey 1987). This factor was not tested in this study. Clearly without such data, the causal mechanisms generating the among cohort variability in increment widths during this study remain speculative.

Intra-cohort trends in increment widths may be related to ontogenic development of *H. castelnaui*. The rapid increase in otolith widths during the first 10–20 d after hatching corresponds to fin ray development, and is also a time of rapid somatic growth (Thorrold 1988). A plateau in otolith spacings is reached after this initial increase, which coincides with attainment of full fin ray complements in the dorsal, anal, and caudal fins. The development of the major locomotory fins suggests increasing mobility as fin rays develop. Coincident development of sensory apparatus (O'Connell 1981) may lead to an exponential increase in the ability of the larvae to catch prey during this period, and hence a similar increase in growth rate.

The transition at the completion of fin ray development cannot be labelled "metamorphosis," as it occurs some 20 d before the beginning of scute and scale development. It does, however, emphasize that metamorphosis need not be the only threshold (sensu Balon 1984) occurring in larval ontogeny. Nonlinearities in growth curves may reflect such ontogenetic events. In *H. castelnaui*, for example, a slowing of growth occurs at a similar age to both full fin ray attainment and the plateau of otolith increment spacings (Thorrold 1988).

The back-calculated growth history of each cohort can be used to interpret differences in the length–age relationship. Cohorts 3 and 4 were larger at a given age than cohorts 1 and 5. The growth trajectories of the individual cohorts suggested that this difference was due to the higher initial growth rates in cohorts 3 and 4, and that this size difference was maintained

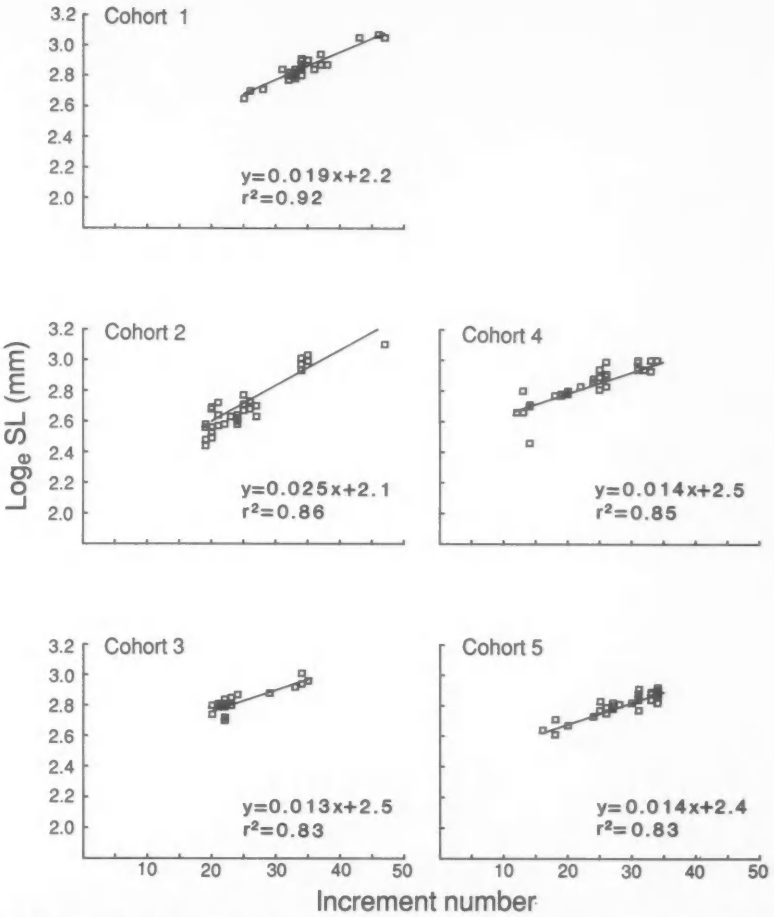

FIG. 6. Relationship between log$_e$ SL and number of growth increments on sagittae for five cohorts of larval *Herklotsichthys castelnaui*. Lines fitted by least-squares linear regression.

TABLE 3. Repeated measures ANOVA table for increment widths with time for: between subjects effects; among subjects effects, and polynomial contrasts for linear and quadratic trends with time. SS = type III sums of squares estimates. Probabilities associated with within subjects effects are corrected according to the Greenhouse–Geisser adjustment factor.

Source	df	SS	*F*-value	$p>F$
Between subjects effects				
Cohort	4	210.73	20.09	0.0001
Error	36	94.41		
Within subjects effects				
Time	24	767.82	82.14	0.0001
Time-cohort	96	141.54	3.79	0.0001
Error(time)	864	336.53	0.389	
Polynomial contrasts with time				
Linear	1	645.23	368.09	0.0001
Cohort	4	19.53	2.79	0.041
Quadratic	1	105.65	122.76	0.0001
Cohort	4	35.90	10.43	0.0001

throughout the first 30 d. Cohort 2 experienced a higher growth rate during days 25–27 than the other cohorts; this apparently was sufficient to alter the length–age relationship of cohort 2 from that of the other 4 cohorts. A caveat is necessary when interpreting such data. A number of studies have documented a decoupling of otolith and fish growth (Bradford and Geen 1987; Mosegaard et al. 1988). These studies reported that otolith growth is conservative in relation to fish growth, and back-calculated growth rates thus underestimated growth variability. It should be noted, however, that both of the above studies were conducted on juvenile fish. Otolith growth in larvae may well respond to changes in somatic growth more quickly; Reckmann and Rey (1987) found otoliths in *Coregonus* spp. larvae responded to changes of ration level and temperature within 1 to 3 d.

In summary, this study suggests that cohorts separated by as little as two weeks may exhibit different growth trajectories. Recent studies of mortality rates in larval fishes have suggested critical events are occurring on spatial scales of 1–100 m, and over temporal scales of hours to days (Fortier and Leggett 1985; Hewitt et al. 1985; Taggart and Leggett 1987). Factors accounting for larval survivorship may be expected to vary on similar

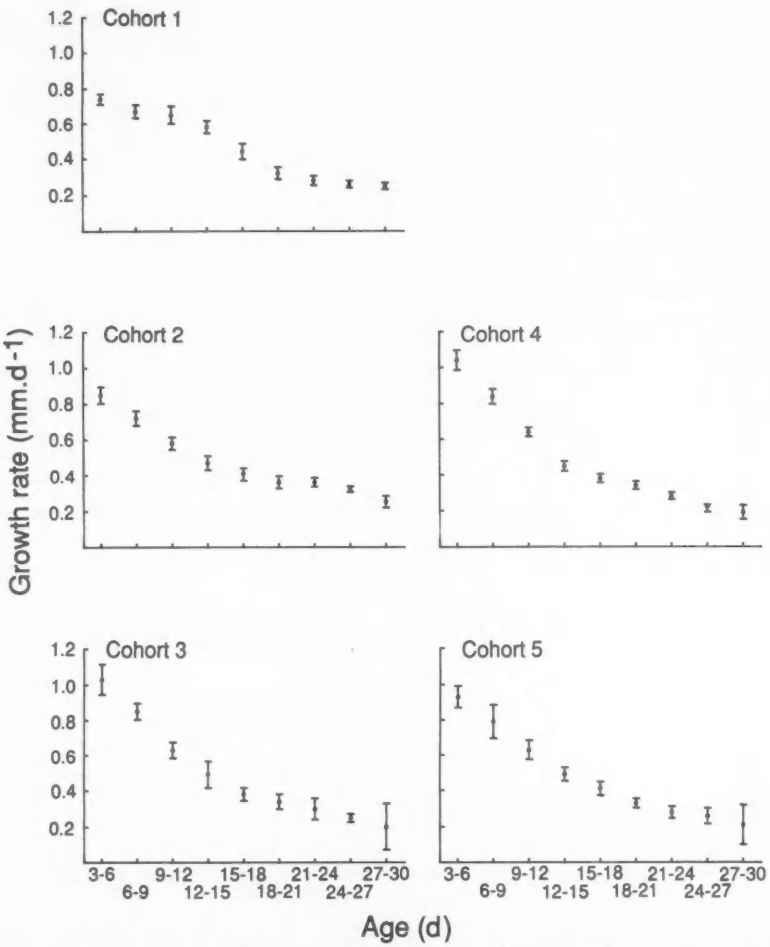

FIG. 7. Growth rates (± standard deviations) of five cohorts of *Herklostichthys castelnaui* larvae averaged over 3 d, estimated from back-calculation of sagittal radii, during the first 30 d of larval life.

TABLE 4. ANOVA results for daily growth rates averaged over 3 d in five cohorts of *Herklostichthys castelnaui* larvae, determined from back-calculation of otolith increment widths (*$p<0.05$; **$p<0.01$; ***$p<0.001$; ns not significant at $p<0.05$). SS = type I sums of squares estimates. Student–Newman–Keuls (SNK) rankings, with increasing mean growth rate from right to left, for $\alpha = 05$, underlined cohorts not different.

Age (d)	df	SS	*F*-value	*p*	SNK ranking
3–6	4	0.973	21.25	***	4=3>5>2>1
6–9	4	0.271	6.89	***	4 3 5 2 1
9–12	4	0.031	1.40	ns	5=4=3=1=2
12–15	4	0.096	4.66	**	1>5=3=2=4
15–18	4	0.041	4.47	**	1>2=5=3=4
18–21	4	0.004	0.52	ns	=2=5=1=4
21–24	4	0.033	4.18	*	2 5 3 1 4
24–27	4	0.033	10.50	**	2 1 5 3 4
27–30	4	0.010	1.64	ns	2=1=5=3=4

scales (Legendre and Demers 1984). Although growth has been suggested as playing a critical role in determining larval survivorship (Houde 1987), growth variability has rarely been documented on these scales (but see Rice et al. 1987). Otolith increment analysis as outlined here provides a way of testing such hypotheses.

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Behavioural Response of the Lobster *Homarus americanus* to Traps

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Karnofsky, E. B., and H. J. Price. 1989. Behavioural response of the lobster *Homarus americanus* to traps. Can. J. Fish. Aquat. Sci. 46: 1625–1632.

A 180-m^2 tank was set up as a semi-natural benthic habitat in order to obtain quantitative visual observations on the behavioural response of lobsters to traps. The wood-lath parlour traps commonly used in the lobster fishery were very inefficient; only 2% of approaches to the traps led to capture. Large (>80-mm carapace length) lobsters (*Homarus americanus*) left before entering the traps in 92% of 428 observed approaches, and were able to escape back out the entrance in 76% of the cases where they actually fed at the bait. Traps baited with thawed mackeral (*Scomber scombrus*) elicited more approaches and captures than did traps containing salted mackeral. Unbaited traps were virtually ignored, indicating they were not attractive as shelter. Lobsters were apparently drawn out of their shelters by the scent of bait, since individuals which lived immediately downstream from the rotating trap positions approached much more frequently than others. However, overall rates of approach and capture varied greatly between lobsters, suggesting that individuals have different motivational levels. These differences could not be explained on the basis of sex or size. Forty percent of the large lobsters were never caught, despite being offered baited traps in 20 separate trials. Longer-term studies are needed to determine whether such individuals will enter traps at different times of year or whether they remain permanently untrapable.

Un bassin de 180 m^2 a été installé dans un habitat benthique semi-naturel afin d'effectuer des observations visuelles quantitatives de la réponse comportementale du homard devant les casiers. Les casiers en lattes de bois couramment utilisés dans la pêche du homard se sont révélés très inefficaces; seulement 2 % des homards qui s'en sont approchés ont été capturés. Les gros homards (supérieurs à 8 mm CL) s'éloignaient avant d'entrer dans le casier dans 92 % des 428 cas d'approche observés; ils ont été capables de ressortir de l'entrée dans 76 % des cas où ils avaient atteint l'appât. Les casiers appâtés avec du maquereau dégelé ont suscité plus d'approches et de captures que ceux contenant du maquereau salé. Les casiers non appâtés ont pratiquement été ignorés, ce qui révèle qu'ils ne présentent aucun attrait à titre d'abri. Les homards étaient apparemment attirés hors de leurs abris par l'odeur de l'appât, puisque des individus qui vivaient immédiatement en aval des casiers s'approchaient beaucoup plus souvent que les autres. Toutefois, les taux globaux d'approches et de captures variaient énormément entre les homards, ce qui laisse croire que les individus ont des degrés de motivation différents. Ces différences n'ont pu être expliquées en fonction du sexe ou de la taille. Quarante pour cent des gros homards n'ont jamais été capturés, malgré qu'on leur ait présenté des casiers appâtés au cours de 20 essais distincts. Des études à plus long terme devront être effectuées pour déterminer s'ils sont davantage susceptibles de pénètrer dans les casiers à d'autres moments de l'année ou s'ils ne n'y pénètrent jamais.

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The lobster *Homarus americanus* supports a multi-million dollar fishery in both Canada and the United States. This fishery is based almost exclusively on the entrance of lobsters into baited traps which are generally deployed for 1–2 d. The behavioural response of lobsters to traps is of interest in assessing the capture efficiency of the traps, the attractiveness of various baits, and the characteristics of individual lobsters which affect trapability. Yet direct observations of trap-related behaviour are rare and usually anecdotal, and have either involved unknown individuals in the field or laboratory observations in small tanks.

Catch statistics and qualitative observations by fishermen suggest that morphological factors such as sex and size influence trapability (Bennett 1974; Ennis 1980). The location of a baited trap relative to shelter locations may also be important. However, it is not clear whether lobsters are drawn out of their shelters by the scent of bait or whether they are trapped only during foraging excursions. It has also been suggested that lobsters will sometimes enter traps for shelter rather than bait. This is of concern due to the possibility of "ghost fishing" by traps which are lost (reviewed by Smolowitz 1984a,b). Lobsters may also prefer certain bait types to others, although many fishermen use both thawed and salted bait (Duggan 1985).

The last factor influencing trapability is the capture efficiency of the trap itself. Behavioural studies on *Cancer* crabs

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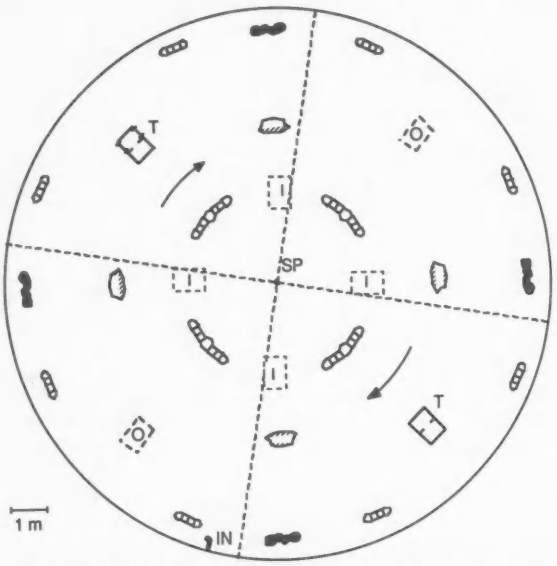

FIG. 1. Schematic diagram of the pool tank layout. Concrete and rock shelters are outlined, stippled areas = mussel clumps, T = traps, SP = standpipe drain, IN = water in-flow. Arrows indicate direction of water flow. Dotted rectangles show alternate trap positions in outer (O) or inner (I) regions of the tank.

and the lobster *Nephrops* suggest that many individuals have difficulty finding the entrance to traps or are frightened away by other individuals prior to entering (Miller 1980; Bjordal 1986). Also, lobsters may be able to escape back out the entrance of traps (reviewed by Elner 1980). The quantitative effect of such factors on the capture efficiency of *H. americanus* is unknown.

There are only a few studies using direct observations of the behavioural response of lobsters to traps. These have either been conducted under unnatural laboratory conditions in small aquaria (e.g. Shelton 1981 on *H. gammarus*), or in situ where the field of view of the video camera was limited and the indentity and history of individual lobsters was unknown (e.g. Bjordal 1986 on *Nephrops norvegicus*). We set up a semi-natural environment for lobsters in the pool tank at Dalhousie University in order to determine the effect of the factors mentioned above on trapability. This large tank covers an area of 180 m^2 and allowed detailed behavioural observation of the response of a complex population of known individuals to trap introduction.

Materials and Methods

Pool Tank

The indoor pool tank at the Aquatron Laboratory at Dalhousie is described in detail by O'Dor et al. (1977). The tank is 15.2 m in diameter and 4 m deep, with a bottom sloping gradually to the center. Ambient temperature sea water was pumped from the Northwest Arm of Halifax Harbor from a depth of 15 m and passed through Graver pressure sand filters before entering the tank. The tank was filled to a depth of 2 m, and a flow-through system was maintained by a single inflow at 150 L/min with a central standpipe for overflow. The angle of the inflow pipe set up a clockwise flow pattern (Fig. 1). Flow velocity around the tank was measured 10 cm off the bottom using a Marsh McBirney Model SN current meter, and ranged from 2.7 cm/s near the center of the tank to 4.8 cm/s at the outer edge. A near-bottom cross-current of 0.5 cm/s flowed from the center to the outer edge due to the central drain at the surface. Water temperature and salinity 10 cm from the bottom ranged from 10.5–13.5°C and 31.9–32.0 parts per thousand (ppt), respectively over 2 mo of the study.

Eight tons of 10-mm granite pea-stone gravel was spread evenly over the bottom forming a 3-cm deep substrate. Although there were no physical barriers in the tank, shelters and food were distributed equally among four quadrants, each with a similar layout (Fig. 1). Groups of cinder blocks, molded concrete structures, and granite rocks were provided for shelter (see Fig. 1 for placement in the tank and dimensions). Cinder blocks have been shown to be suitable shelter for lobsters in both laboratory (Atema et al. 1979) and field (Sheehy 1976) studies. The molded concrete structures were large enough for two individuals and were patterned after those used in mating studies (Atema et al. 1979). Both the cinder blocks and molded concrete shelters had two openings, as has been observed in lobster shelters in the field and in preference studies in the laboratory (Cobb 1971).

Mussels (*Mytilis edulis*) and sea urchins (*Strongylocentrotus droebachiensis*) were supplied as prey. Elner and Campbell (1987) found that mussels were a dominant component of the gut contents of *Homarus americanus*. Although they found that sea urchins were a minor component, there has been considerable controversy over whether lobster predation has a significant impact on sea urchin populations (e.g. Breen 1987; Miller 1987). Mussel clumps were placed on four equally spaced rock groups at the periphery of the tank (Fig. 1). Each site was replenished with approximately 2 kg of mussels every 10 d. Several thousand sea urchins were introduced and dispersed themselves throughout the tank. Kelp (*Laminaria longicruris*) fronds served as food for the urchins. These fronds were placed in 12 locations, covering a total of <2% of the area of the tank and were replenished as necessary.

Artificial light was provided by 24 400-W Sylvania Metalarc Lamps 6 m above the water surface and eight 100-W incandescent bulbs. There were three light levels: "day" (3.4 $\mu E \cdot m^{-2} \cdot s^{-1}$, 0400–1800 h), "dusk" (0.25 $\mu E \cdot m^{-2} \cdot s^{-1}$, 1800–2100 h), and "night" (0.03 $\mu E \cdot m^{-2} \cdot s^{-1}$, 2100–0400 h). This roughly approximated the photoperiod at this latitude while providing an extended dusk period for behavioural observations.

Lobsters

Lobsters were collected using traps and SCUBA off Pictou and Lunenberg, Nova Scotia. Lobsters were held 1–14 d in tanks with running sea water and were fed mussels ad libitum until they were introduced into the pool tank. The carapace length (CL) of each lobster was then measured and they were checked for injuries. Animals with injured claws, antennae, or antennules were not used, nor were individuals which were soft-shelled or carrying eggs. Individuals which were selected were labelled with numbered bands behind the dactyl of the large claws to allow easy indentification (lobsters often sit at the entrance of a shelter with their claws visible) without interfering with claw use. The tips of various pleura were clipped in unique numerical combinations for indentification following a molt.

Thirty lobsters (*H. americanus*) were introduced into the tank in July 1987 including six large males (95.0–118.0 mm CL),

12 large females (83.2–112.0 mm CL), six small males (62.0–70.8 mm CL) and six small females (60.9–69.4 mm CL). All individuals survived to the end of the 2-mo study. Large females were the most abundant category since we wanted to maximize our chances of observing matings which occur at the female's molt for use in a concurrent study. The area of the pool tank is 180 m^2 therefore there was a population density of 0.17 lobsters/m^2, which compares reasonably with field reports (Stewart 1970; Karnofsky et al. 1989). However, given the number of large lobsters in our study, the total biomass exceeded that found in the field.

Trapping

Wood-lath parlour traps were used (base = 86.0 by 55.5 cm, height = 38.0 cm) with net funnel entrances (width = 27.5 cm, height = 18.0 cm) held open with 13.0-cm diameter wooden rings. The entrances open into the "kitchen" which contains the bait. Behind the bait a long funnel leads to a second compartment, the "parlour", which contains two escape vents (width = 18.0 cm, height = 4.5 cm), large enough to allow lobsters <80 mm CL to escape. Traps were introduced in pairs, one on each side of the tank, between 1000 and 1200 h and were left in place for 24 h. Bennett (1974) showed that most lobsters are caught in the first 24 h after a trap is set. When the traps were pulled, individuals in the trap were recorded and returned immediately to the tank. We then waited 24 h before introducing another pair of traps. Over the course of the study the position of the trap containing thawed mackeral was rotated around the tank so that each quadrant was treated equally. The first 12 trials compared an unbaited trap with a trap baited with thawed mackeral (*Scomber scombrus*) to examine the possibility that traps are used for shelter as well as food. In each trial an approximately 300-g piece of mackeral (the anterior half) was impaled on a wooden spike in the kitchen. During eight of these trials traps were placed near the periphery of the tank (O's in Fig. 1) and during four they were placed near the center (I's in Fig. 1). The last eight trials compared thawed with salted mackeral (prepared by a local lobsterman) as bait, and were conducted near the center of the tank.

The traps were observed with binoculars for 1 h and 20 min after their introduction in the morning and for 2 1/2 h during the dusk light level. Traps were also observed during four 20-min censuses which were taken every day to determine where the lobsters were in the tank and what they were doing. Combining the different observation periods we accumulated a total of 103 h of observations on trap-related behaviour. All approaches to the trap and subsequent trap-related behaviours were recorded, including the identification number of the individual and interactions with other lobsters near the trap. During the last four trials lobsters were also timed with a stopwatch from the moment they touched the downstream side of the trap until they were 1 m away from the opening. Since individuals could be recognized throughout the study, Wilcoxon Signed-Rank test on paired observations was used to examine the response of individuals to various treatments.

Results

Capture Efficiency

Lobsters nearly always approached baited traps from the downstream side, turning towards the trap when they entered a region 1 to 2 m away. Since we never observed any individuals entering the trap through the upstream entrance, we defined a trap approach as any instance when a lobster walked within 1 m of the downstream side. Lobsters appeared wary of the trap and many avoided it without touching it. When individuals touched the trap, they generally moved along the edge to a position immediately downstream of the bait. They often stood at this position for periods ranging from 1 to 5 min, attempting to reach the bait by poking their claws through the wooden slats. In many instances they also poked their claws through the net leading to the trap entrance, or climbed part way up the net without entering. Some individuals reached past the wooden ring at the end of the funnel, hooking their telson over the edge of the ring. This enabled them to hang down into the kitchen to feed on the bait, then pull their bodies back out onto the net and leave. Lobsters which completely entered the kitchen generally fed at the bait for several minutes, then began attempting to escape by poking their claws through the slats in the kitchen. Some of these individuals were able to find their way back out the entrance, and on two occasions we saw individuals tear the bait entirely off the stake and remove it from the trap. Other individuals passed through the funnel to the parlour after feeding. Small lobsters (<80 mm CL) were able to leave the parlour through the escape vents, but large lobsters were never able to escape after entering the parlour.

TABLE 1. Comparison of thawed versus salted mackeral as bait in eight trials when both were presented.

	Thawed	Salted	Wilcoxon-*t*
Mean and range of number of approaches per individual	12.4 0–47	6.4 0–20	47 $P<0.01$
Mean and range of time spent at trap ($s \cdot individual^{-1} \cdot approach^{-1}$)	65.6 2–638	29.4 1–259	58 $P<0.01$
Number of individuals captured at least once	7	1	2 $P<0.05$

Lobsters which left the traps prior to touching or entering often did so in response to other lobsters approaching. These interactions rarely involved physical contact. Submissive lobsters retreated or were chased away when another lobster approached.

Traps containing no bait were generally ignored by the lobsters, eliciting only seven approaches and no captures. Baited traps containing salted mackeral were much less attractive than traps with thawed mackeral. Lobsters approached less, spent less time at the trap and were captured less frequently in traps baited with salted mackeral (Table 1). The presence/absence of salted mackeral in the alternate trap apparently had no effect on the rate of approach (Wilcoxon $T = 188$, $n = 28$, $P > 0.05$) and capture (Wilcoxon $T = 25$, $n = 10$, $P > 0.05$) for the trap containing thawed mackeral. Because of these factors, the remainder of our data are calculated from all of the traps containing thawed mackeral ($n = 20$), regardless of whether the alternate trap was empty or contained salted bait, unless otherwise indicated.

The capture efficiency of the traps was examined by quantifying each of the steps in the behavioural sequence from approach to capture described above for each individual lobster (Table 2) and for the large lobsters as a group (Fig. 2). These calculations are based on pooled data for all traps located in both the inner and outer portions of the tank. Since small lobsters left through escape vents the sequence in Fig. 2 is reported for large lobsters only. Lobsters left without entering

TABLE 2. Behavioural sequence from approach to capture. Numbers shown are the observed occurrences for each individual. M = male, F = female, CL = carapace length.

Sex	Size (CL)(mm)	Approach	Touch	Enter	Observed capture	Total capture
M	118.0	26	21	2	0	0
M	116.0	26	23	1	0	0
M	102.4	20	14	3	0	4
M	100.5	14	5	0	0	0
M	99.0	33	25	1	1	3
M	95.0	39	33	7	2	5
F	112.0	38	33	4	0	1
F	101.2	7	4	0	0	0
F	96.7	38	27	0	0	1
F	94.7	54	42	2	1	7
F	92.9	8	6	0	0	0
F	91.3	1	0	0	0	0
F	91.0	49	36	4	1	1
F	89.2	6	3	1	0	1
F	85.4	3	2	0	0	0
F	85.0	13	12	2	1	3
F	84.5	30	16	2	0	2
F	83.2	23	18	5	2	4
M	70.8	24	16	11	0	0
M	69.3	8	5	1	0	0
M	67.9	40	29	0	0	0
M	67.5	50	28	0	0	0
M	63.7	22	19	4	0	0
M	62.0	15	4	0	0	0
F	69.4	0	0	1	0	0
F	66.0	1	1	0	0	0
F	65.7	7	1	0	0	0
F	65.0	5	2	0	0	0
F	62.8	51	29	2	0	0
F	60.9	7	2	0	0	0

in 92% of observed approaches. An entry was counted whenever a lobster was far enough into the trap to feed at the bait. Of those that left without entering, 30% did so in response to agonistic interactions with other lobsters. The majority of individuals which actually fed at the bait were able to do so without being captured. The ultimate effect of the factors outlined in Fig. 2 is that only 2% of the approaches to the trap by large individuals resulted in capture. Also, only 11 of the 18 large individuals present in the tank were captured during our study, although they were offered baited traps in 20 separate trials.

Variability Between Individuals

The total number of observed approaches pooled over all the trials varied by as much as an order of magnitude between large individuals, and the number of times each individual was captured ranged from zero to seven (Table 2). Large individuals which approached more tended to be caught more (Kendall's Tau, $Z = 2.46$, $P < 0.01$, Fig. 3), although there were numerous exceptions. The observed number of times large individuals fed at the bait and left ranged from zero to five. A high level of variability was also evident between the small individuals. Approaches per individual ranged from one to 51 (Table 2). Five of 12 small lobsters were observed feeding at the bait and leaving through the escape vents at least once during the 20 trials. Of these, three fed and left repeatedly.

Two-way ANOVA with repeated measures on one factor (Winer 1971) was used to test for variability between categories of lobsters while accounting for differences between individuals and within individuals over time. No significant differences were found in the rates of approach or entry to traps based on categories of sex or size (F-tests, $df = 1, 28$, $P > 0.05$). Of the seven females which extruded eggs during the study, four were caught at least once. Of the three large lobsters which molted during the course of the study one was caught, and capture occurred 3 wk after the molt. The sample size was too small to test the effect of these factors on capture rates.

Since 11 of the large lobsters in our study were returned to the tank after at least one capture, we also looked for evidence that the behaviour of these individuals might differ due to capture. The rate of approach to traps did not differ between trial days before and after an individual was first captured (Wilcoxon $T = 8$, $n = 6$, $P > 0.05$). Also, several individuals which were caught once were never caught again while others were caught repeatedly (Table 2). Thus there is no evidence that capture led to subsequent avoidance or attraction to the traps.

Effects of Trap Position

Approach rate did not vary between traps placed in different quarters of the tank ($X^2 = 0.37$, $P > 0.05$). However, approach rate greatly increased when traps were moved from the sparsely populated outer portion of the tank to the inner portion where more shelters were in close proximity to trap locations (Figs. 1 and 4). Surprisingly, Fig. 4 indicates that although approach rate by large lobsters increased in the inner trap positions (Wilcoxon $T = 50$, $n = 29$, $P < 0.001$), there was no corresponding increase in capture rate (Wilcoxon $T = 26$, $n = 11$, $P > 0.05$).

The effect of shelter proximity in the inner circle was examined more directly by comparing the approach rate for each individual to the location of its shelter immediately prior to trap introduction, using the trials when only thawed mackeral was present. Individuals approached more when they were living in the shelter group immediately downstream from the baited trap ($\bar{x} = 0.90$ approaches·lobster^{-1}·h^{-1}) than when they were living in other shelter groups in the inner circle ($\bar{x} = 0.38$ approaches·lobster^{-1}·h^{-1} (Wilcoxon $T = 1$, $n = 6$, $P < 0.05$). Lobsters did not appear to move into shelters closer to the trap. On the contrary, individuals were less likely to be seen in the shelter group immediately downstream from the trap during the 24 h the trap was present (4.5% of the censuses) than during the 24 h before trap addition (8.2%) (Wilcoxon $T = 18$, $n = 13$, $P < 0.05$).

Temporal Changes

The temporal pattern of approach varied depending on whether traps were placed in inner versus outer portions of the tank. The approach rates were calculated using the pooled data set consisting of the total number of approaches by both large and small lobsters to traps containing either thawed or salted mackeral. Lobsters approached traps placed at the periphery of the tank at a higher rate during the dusk observation period ($\bar{x} = 0.1$ approaches·lobster^{-1}·h^{-1}) than during the morning observation period immediately following trap introduction ($\bar{x} = 0.04$ approaches·lobster^{-1}·h^{-1}) (Wilcoxon $T = 26$, $n = 17$, $P < 0.05$). This pattern was reversed when traps were placed in the inner portions of the tank. In this location, approach rate during the daytime observation period ($\bar{x} = 0.8$ approaches·lobster^{-1}·h^{-1}) was significantly higher than during

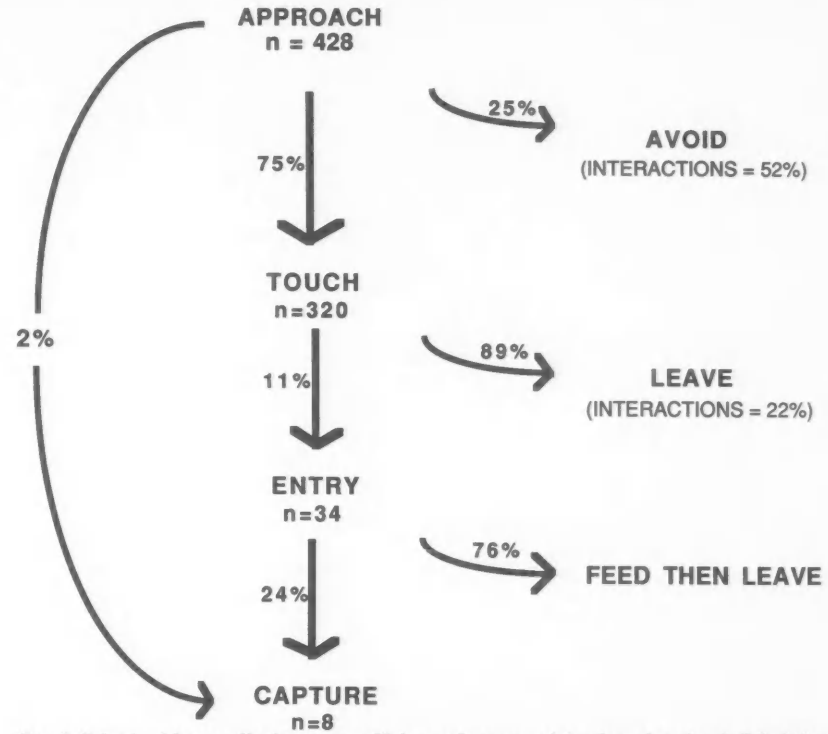

FIG. 2. Behavioral factors affecting capture efficiency of traps containing thawed mackeral. Calculations are based on approaches by large lobsters only, and captures were included only if they occurred during an observation period. Interactions are the percentage of lobsters that avoided or left the trap after touching due to an interaction with another approaching individual.

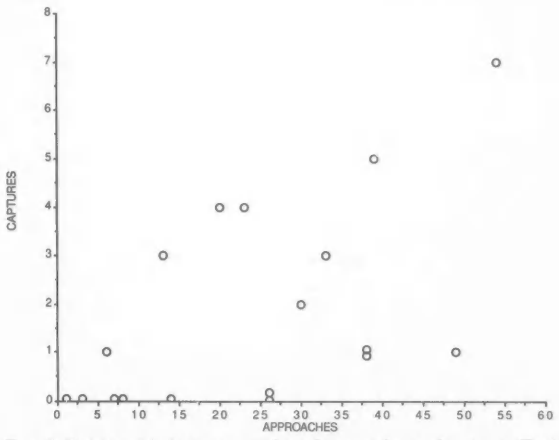

FIG. 3. Relationship between number of approaches and captures. Each point shows the total for a single large lobster summed over all trap trials.

the dusk hours ($\bar{x}=0.3$ approaches·lobster^{-1}·h^{-1}) (Wilcoxon $T=61$, $n=28$, $P<0.005$). However, the number of captures over the whole study which occurred during the day (17) did not vary from the number of captures at night including dusk (16).

Lobsters began to respond immediately when traps were introduced in the inner circle, presumably due to detection of a new scent trail. Observed approaches were high during the first 10 min after introduction ($\bar{x}=7.3$/trial), while mean approaches over the next seven 10-min intervals only ranged from 2.3 to 4.3 per trial. On a finer temporal scale, approach rate also varied due to the behaviour of individuals at the trap. The process of tearing at the bait while feeding apparently released odors which attracted other individuals. On average an individual was twice as likely to approach the trap during the 20-min interval after another lobster fed at the bait than during the preceeding 20 min (Wilcoxon $T=24.5$, $n=21$, $P<0.005$). The presence of baited traps also seemed to draw some individuals out of their shelters. There was a small but consistent increase in the percent of census observations in which each individual was out of shelter during the 24 h of trap immersion ($\bar{x}=33\%$) than during the preceeding 24-h periods ($\bar{x}=30\%$) (Wilcoxon $T=85$, $n=29$, $P<0.005$).

Discussion

Capture Efficiency

The mean catch rate of 1.6 large lobsters per trap obtained in this study is within the range of catch rates observed in the field. There is great variability in catch rates reported in the literature (Estrella and McKiernan 1986; Miller 1989), both between regions and over time. However, the conditions of our

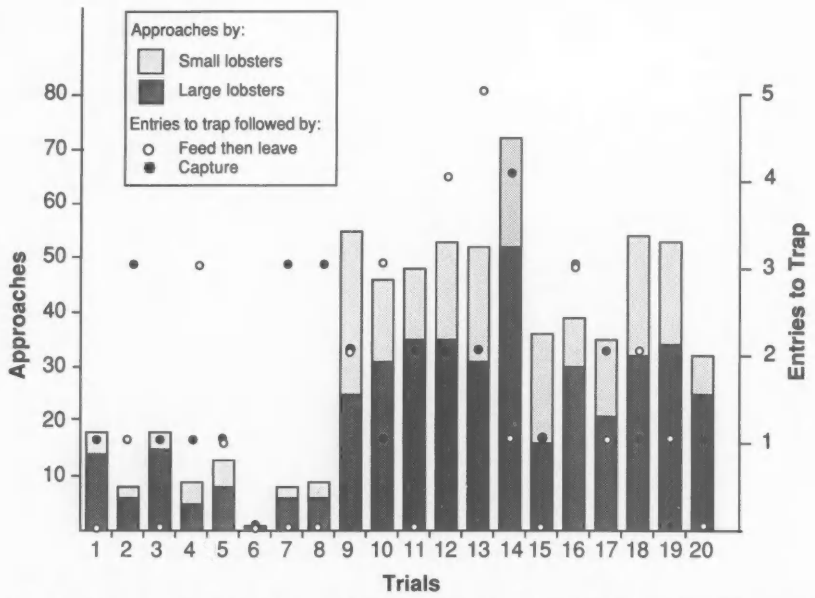

FIG. 4. Observed approaches, instances of feeding and leaving, and total captures for each trap trial. The first eight trials were conducted in the outer portions of the tank, while the last 12 were conducted in the inner positions. Number of approaches and feed then leave are based on both small and large lobsters, while captures are for large lobsters only.

experiment may have optimized captures in the tank due to a number of factors discussed below. The tank, although quite large, is not comparable to field conditions where individuals can wander far out of range of the odor trails. Also, the lack of predators in the tank may have made individuals less wary of being exposed out of their shelters.

Traps were oriented in the tank with the entrances in line with the current, so that the odor of the bait passed close to or through the downstream entrance. Miller (1980) examined the effect of trap orientation relative to current direction for crabs, and found that the percentage of approaching individuals which entered was greatest if the trap entrance was directly downstream from the bait. Crabs apparently had difficulty locating the entrance, and were often unsuccessful unless the odor trail led them directly to it. In this study, lobsters spent considerable time trying to reach the bait through the wooden slats directly downstream prior to leaving the trap or climbing in the net entrance. If the odor trail had not passed near an entrance, the lobsters probably would have had even more trouble locating it. Shelton (1981) also stressed the importance of making it easier for lobsters to find the entrance based on observations of *Homarus gammarus* in large aquaria. Capture efficiency under otherwise comparable conditions in the field would undoubtedly be lower since fishermen have little control over trap orientation.

Capture rates in our study may also have been influenced by the low diversity of food available in the tank. Elner and Campbell (1987) showed that lobsters on barren ground habitats maintain a gross dietary composition which is remarkably similar to that of lobsters in macroalgal habitats, despite large differences in the relative abundance of available prey. Lobsters appear to feed selectively, and their nutritional requirements may be more readily met by a diversity of prey types. Therefore, lobsters in our study may have been more attracted to the bait due to the restricted range of prey types available to them, i.e. mussels and sea urchins.

Despite these factors which theoretically should have optimized capture rates in our tank, the traps were very inefficient. The perfect trap would catch each lobster on its first approach (Miller 1980). However, only 2% of the observed approaches by large lobsters resulted in capture. Many lobsters avoided the trap without touching it, and of those that did touch, the majority left without entering. Interactions between individuals were a major factor in lobsters leaving the trap area before entering. Of the lobsters which fed from the bait, 76% were not captured.

The basic design of the wooden lobster traps deployed by most fishermen has remained essentially unchanged for over 100 yr (Elner 1980). The inefficiency of the traps shown in our behavioural observations suggests a number of potential design modifications. The number of lobsters which leave a trap without entering might be reduced by using traps with entrances which funnel individuals from a larger proportion of the trap base. Such a trap is currently under development (R. Duggan, pers. comm.). The number of individuals which can feed at the bait while keeping their telson locked over the entrance ring might be reduced through the use of larger traps or bait containers which are difficult to manipulate. Shutters on the entrances might prevent escapes from the kitchen, although in snow crab traps, shutters, while preventing escape, lowered catch rates (Anon. 1969, cited by Elner 1980). The parlour appeared to be the most efficient device for retaining lobsters. This has also been shown for *H. gammarus* by comparing catch rates for different types of traps (Gibson and Hefferman 1967).

Low capture efficiency is apparently not limited to this particular trap design, tank, or lobster species. Bjordal (1986)

used an underwater video camera mounted over a trap to monitor the approaches and captures of *Nephrops norvegicus* in the field. Sixty-five percent of the individuals which approached the trap left without touching it, and only 6% of the individuals which approached were caught. Bjordal suggested that *Nephrops* had difficulty locating the trap entrance, and may have been wary of the trap since it was an unnatural environmental factor. He also reported agonistic interactions between individuals converging on a trap, as did Miller (1980) for crabs.

The presence of bait had an obvious effect on capture rates. Very few lobsters approached the unbaited trap and none attempted to enter it. There has been some concern over the degree to which lobsters enter unbaited traps due to evidence of "ghost fishing" by lost traps (Pecci et al. 1984; Smolowitz 1984a). In environments with fewer shelter possibilities such as sand flats or barrens, lobsters may enter traps for shelter, but in this environment they did not.

Traps with salted bait were much less attractive than those with thawed bait, as illustrated by the low approach rate, shorter time spent at the trap and the single capture. Similarly, Thomas (1966) found that fresh mackeral caught 2.6 times more *H. gammarus* that did salted bait. Our results differ from those of Daniel and Bayer (1987), who offered leachates from various bait types to postlarval stages of *H. americanus* in small aquaria. They found no difference in the "attractiveness" of leachates from thawed versus salted herring. However, the behavioural assay they used to estimate attractiveness included the presence of maxilliped motions and periopod scooping. Such relatively low-key behaviours may not be adequate indicators of bait preferences since a higher motivational level is probably required for an individual to approach and enter a trap.

Sublegal-sized lobsters were not caught in this study due to the presence of escape vents. However, these vents may increase the long-term capture efficiencies for larger lobsters by conditioning small individuals to enter the trap, and particularly to enter the parlour. Since small lobsters which entered the parlour generally found the escape vents quite rapidly (<1 min), they may not have been unduly disturbed by their temporary capture. On several occasions we saw small lobsters leave the escape vents and head directly back to the entrance of the trap. Such training should increase the chances of a lobster being caught after it molts to legal size. Escape vents have been shown to increase the catch of legal lobsters at the same time as decreasing the catch of sub-legals (Fogarty and Borden 1980), therefore there is no disadvantage in allowing small lobsters to leave the parlour.

Odor Detection

Odor detection involves detecting a chemical stimulus (signal) above the background level (noise) of molecules present in the water column. When an odor source (bait) enters the water, molecules released from the source are carried downstream in the current. Chemicals are continually released and occasionally there is a pulse as in the initial entry of the trap into the water or when the bait is disturbed. Lobsters detect and behaviourally orient to changes in the stimulus gradient (McLeese 1973).

When the trap was introduced into the tank the odor pulse elicited a flurry of approaches. Approach rate also increased when a lobster was feeding at the bait. Many lobsters <80 mm CL in our study entered the trap to feed then left through the escape vents in the parlour. In addition to the training effects described above, the behaviour of small lobsters may benefit the fishery by releasing odor from the bait, thereby increasing the attractiveness of the trap. Conan et al. (1984b) suggested that fish which incidentally enter the trap may be helpful in the same way by releasing odor as they tear at the bait.

In order to respond to an odor, concentrations must reach a physiological detection threshold and a behavioural response threshold. Chapman and Howard (1979) suggest that the odor of bait does not induce the lobster *N. norvegicus* to leave its shelter, and that attraction to the trap only occurs if an animal is stimulated during a feeding excursion. This suggests that response to detected odors depends upon the individual's motivational state. In our study, when a trap was placed in the outer portion of the tank, approach rate was higher during the dusk than during the daytime observation period. This pattern was reversed when the trap was placed in the inner portion of the tank. Lobsters are less active in the daytime (Ennis 1984; Lawton 1987), and a stronger bait stimulus may be needed to overcome this tendency. More lobsters inhabited shelters in the inner than in the outer portions of the tank (Karnofsky and Price 1989), and inner shelter positions were closer to trap locations. When traps were closer to the lobsters' shelters, they approached during the day. When traps were further away resulting in a reduced odor, lobsters may have detected the traps in the outer positions only during crepuscular excursions, since more individuals were observed walking during dusk (Karnofsky and Price 1989). The effect of odor intensity is also evident in direct comparisons of an individual's shelter location with its approach rate. During the inner trials, individuals approached more often if they were living in the shelters immediately downstream. This support Elner's (1980) statement that the "proportion of the population responding to bait may be expected to decline with distance approximately according to the inverse square law".

Individual Variability

Although approach was correlated with capture in large lobsters, there were numerous exceptions. For example, three individuals were observed approaching the trap 38–49 times, but were only caught once throughout the course of the study. Since we only observed the traps for approximately 20% of their immersion time, the actual number of approaches for these and all other lobsters was undoubtedly much greater. Approaches by these three individuals account for 45% of the observed increase in total approaches when traps were moved from the outer to inner portions of the tank.

Attempts to explain individual variability in approach and entrance rates on the basis of size and sex were unsuccessful. The high degree of variability between lobsters suggests that individuals have different motivational levels. Thus the sample size in our experiment may have been inadequate to detect real differences between sex and size categories. Differences in motivation may be influenced by physiological cycles such as molting. Ennis (1978) found that the proportion of recently molted lobsters in SCUBA collections was greater than in trap collections. In our study, of the three large lobsters that molted, one was captured. Presence of extruded eggs did not seem to be a factor, since there was no difference in the fraction of berried and unberried females which were caught.

For the most part, the variation between individuals in the approach and capture rates seen here can not be explained by

any obvious morphological or physiological characteristics. Behavioural differences between apparently similar individuals should not really be surprising; they have been found in almost every ethological study in which individuals could be recognized (Slater 1981), including many on invertebrates (e.g. Aldrich 1986; Hazlett 1978; Mackas and Burns 1986). For lobsters, as with most invertebrates, it is not known whether variability is due to individuals which have similar behavioural cycles but are cycling out of phase, or whether there are components of the population which consistently behave differently.

Approximately 40% of the large individuals in the tank were never caught despite being offered baited traps in 20 different trials. It has been hypothesized that certain lobsters may be untrapable due to genetic shifts caused by fishing pressure (Fogarty and Idoine 1986; Conan et al. 1984a). Future studies on trapability should be conducted over longer time spans, preferably at least 1 yr. Such studies could determine whether apparently untrapable individuals will enter traps at other times of the year, or whether they remain permanently untrapable. This question has important implications regarding the use of catch statistics for estimating population size, since most studies assume that 85% of the field population of legal-sized lobsters is caught over the course of the annual fishing season (Anthony 1980; Campbell 1980).

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Event Analysis Applied to Timing in Marine Fish Ontogeny[1]

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Chambers, R. C., and W. C. Leggett. 1989. Event analysis applied to timing in marine fish ontogeny. Can. J. Fish. Aquat. Sci. 46: 1633–1641.

We illustrate the utility of event analysis for characterizing timing in marine fish life histories, comparing event series among experimental groups, and predicting event timing in untested environments. Two examples using early life history traits are given. In example (1) we analyzed parental influence on metamorphosis timing in experimental laboratory populations of winter flounder (*Pseudopleuronectes americanus*). We fit a Weibull distribution to right-censored observations of age at metamorphosis and then estimated the fraction of individuals from each of two families that had become juveniles by a predetermined day. Offspring of one family were 1.25 times more likely than the second to enter the juvenile period under the applied time constraint. In example (2) we evaluated temperature effects on age at death of unfed capelin hatchlings (*Mallotus villosus*). Using an accelerated failure time model we predicted age at death at an untested temperature and, assuming a patchy distribution of prey, estimated the number of days available to a cohort to encounter a suitable food patch and still maintain the potential for generating an above average year-class. These examples demonstrate the utility of event analysis for more thorough use of observations on ontogenetic timing in experimental and natural populations.

Cet article illustre l'utilité de l'analyse événementielle dans la caractérisation de la chronologie des cycles de vie des poissons marins, en comparant des séries d'événements au sein de groupes expérimentaux et en prévoyant la chronologie des événements dans des milieux non testés. Deux exemples faisant appel à des traits du début du cycle de vie sont donnés. Dans l'exemple 1, les auteurs analysent l'influence parentale sur la chronologie de la métamorphose dans des populations de laboratoire expérimentales de plies rouges (*Pseudopleuronectes americanus*). Ils ajustent une distribution de Weibull à des observations de l'âge à la métamorphose, puis estiment la fraction des spécimens de chacune des deux familles passés au stade juvénile à partir d'une journée prédéterminée. Les petits d'une famille avaient 1,25 fois plus de chances que ceux de la deuxième de passer au stade juvénile compte tenu de la contrainte temporelle. Dans l'exemple 2, les auteurs ont évalué les effets de la température sur l'âge à la mort de petits capelans (*Mallotus villosus*) non nourris. À l'aide d'un modèle temporel d'échec accéléré, les auteurs ont prédit l'âge à la mort à une température non testée et, en supposant une distribution par tache des proies, ont estimé le nombre de jours qu'avait une cohorte pour trouver une source d'aliments convenables et pour rester capable de produire une classe annuelle au-dessus de la moyenne. Ces exemples démontrent l'utilité de l'analyse événementielle pour une utilisation plus exhaustive des observations de la chronologie ontogénétique dans les populations expérimentales et naturelles.

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The timing of the early life history transitions in marine fishes is believed critical to probability of survival of the individual. Transitions, such as hatching or metamophrosis, are times of radical change in morphology, ecology, and behaviour (Moser 1981; Balon 1984; Chambers et al. 1988; Youson 1988). It is often of value to the biologist to compare the timing of such events in two or more species, populations, or experimental groups.

Here we describe and apply methods to characterize and compare timing of transitions in marine fish life histories. We use techniques, referred to as event analysis, wherein the entire distribution of event times, rather than simply mean or median times, are used. This allows more efficient and complete depictions of event schedules than currently achieved. For example, ages at hatching, yolk depletion, first feeding, and death of unfed larvae are frequently reported (see reviews in Blaxter 1969, 1988; Hempel 1979). Plots of event occurrence versus age are common (Lasker et al. 1970; May 1971; Iversen and Danielssen 1984). Alternatively the median or mean ages at these events are listed without further analysis (Smigielski et al. 1984; Oozeki and Hirano 1985; Bagarinao 1986). In some cases median ages are fitted to curvilinear functions, as is common for temperature effects on hatching (Lasker 1964; Williams 1975; Zweifel and Lasker 1976; Hunter and Kimbrell 1980; Frank and Leggett 1981; Laurence and Howell 1981; Howell and Caldwell 1984; Yamashita and Aoyama 1985). Graphical or tabular presentation of medians, or a least-squares fit to these, ignores treatment effects on event dispersion. This restriction may be inconsequential for some hypotheses where effects simply shift the event distribution. However, even with such responses the assumption of same shape is rarely validated. These approaches are more obviously deficient where treatments influence events in subtle or complex ways (e.g. fish from two or more natural populations, brood stocks, diets, or sublethal doses of toxins). Moreover, measures of central tend-

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ency may be less important than measures of dispersion because variation in event timing may be more predictive of survival or other measures of performance.

Event analysis has been developed to analyze product reliability and failure time (Mann et al. 1974; Kalbfleisch and Prentice 1980; Lawless 1982; Nelson 1982; Cox and Oakes 1984) and applied to survival and remission times in clinical trials (Gross and Clark 1975; Lee 1980) and job duration, move frequency, and recidivism in sociological studies (Allison 1984). For analysis of event data in other ecological contexts and with data structures different than those considered here, see Pinder et al. (1978); Siler (1979); Muenchow (1986); and Pyke and Thompson (1986).

We first describe methods to characterize and compare event schedules, and then demonstrate parametric event analysis by two examples. In example (1) we analyze timing of metamorphosis in laboratory populations of winter flounder (*Pseudopleuronectes americanus*) that differ in parentage. We fit distributions to observed ages at metamorphosis, test for differences between like distributional parameters for the two families, and provide an application of this approach by evaluating consequences of differential parental effects on metamorphosis timing of progeny occupying a hypothetical temporary habitat. In example (2) we analyze survivorship curves of laboratory populations of unfed capelin hatchlings (*Mallotus villosus*) maintained at three constant temperatures. We fit distributions to survival data and estimate the magnitude of the temperature effect on expected lifetime. We predict age at death of larvae at temperatures untested in our experiment by use of a failure time model and apply this result to estimate the likelihood of a strong year-class being formed assuming patchy prey distribution and a threshold criterion of survival necessary to generate a strong year-class.

Characterizing Event Distributions

The data necessary for event analysis are times at which individuals undergo the event. Such times have associated variation and distributional properties. These attributes are retained in event analysis. Furthermore, sampling often terminates before some individuals undergo the event or previously monitored individuals may be lost from sampling. Time-at-event observations for these individuals are termed censored. These individuals are considered at risk of undergoing the event and, hence, contribute to estimates of event distribution parameters. The last recorded ages of these individuals are simply coded for their termination or disappearance status.

Event Functions

Time at occurrence of an event is represented by T (>0). For this development we claim the event to be death but the logic holds for any variable with positive values. Three functions are often used to characterize event times.

(i) The survival function, $S(t)$, defined as

$$(1)\quad S(t) = \text{Prob}\{\text{an individual survives} > t\} = \text{Prob}\{(T > t\},$$

is the most familiar and is commonly manifest as a survivorship curve (Fig. 1A). The cumulative ffequency distribution (c.d.f.), which is the complement of $S(t)$, is the function of interest in many applications (example (1), below).

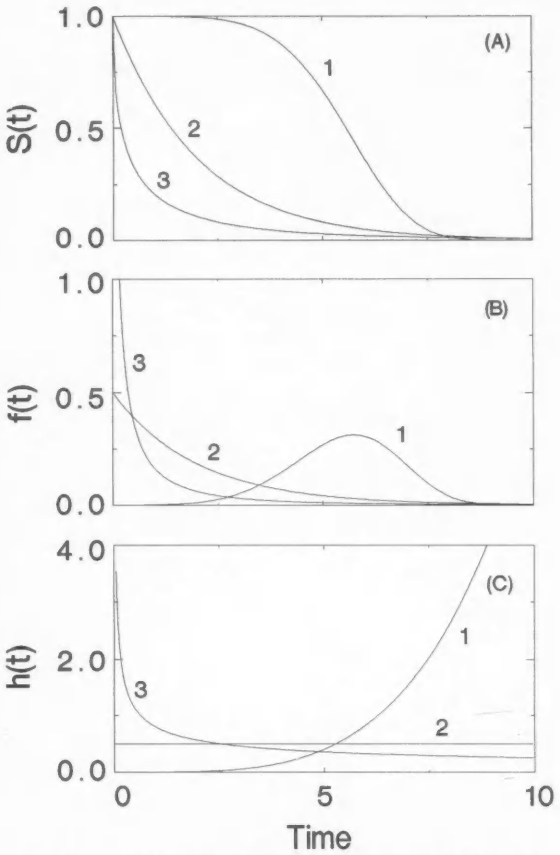

FIG. 1. Survival (A), probability density (B), and hazard (C) functions of event data as modelled by Weibull distributions. Scale and shape parameter values for each of the three curves are (1) $\alpha = 6$, $\gamma = 5$; (2) $\alpha = 2$, $\gamma = 1$; and (3) $\alpha = 0.4$, $\gamma = 0.5$. Numbers that label each curve also correspond to Deevey's (1947) Type I, II, and III survivorship curves.

(ii) The probability density function (p.d.f.) of T, $f(t)$, gives the probability that an individual dies within a small time interval,

$$(2)\quad f(t) = \lim_{t \to 0} \frac{\text{Prob}\{\text{an individual dies in interval } (t,\ t+dt)\}}{dt}$$

$$(2')\quad \int_{t=0}^{t=\infty} f(x)\,dx = 1 = F(t),$$

where $F(t)$, is the c.d.f. of mortality.

(iii) The hazard function, $h(t)$, is a conditional mortality rate defined as,

$$(3)\quad h(t) = \lim_{t \to 0} \frac{\text{Prob}\{\text{an individual age } t \text{ dies in interval } (t,\ t+dt)\}}{dt}$$

This hazard is conditional on the individual reaching age t (i.e. an age-specific mortality rate) and is the instantaneous mortality rate in fisheries (Fig. 1C). These event functions (equations (1–3)) are interrelated; given any one the other two can be derived (appendix 1). Each event function uniquely characterizes an event distribution and each presents data in a way that allows the posing of different questions. For example, percen-

tiles of the survivorship curve can be derived from the survival function, the interval of maximum number of deaths can be found from the p.d.f., and the age at which an individual is at greatest risk of death can be determined from the hazard function.

Analysis of Event Distributions

Exponential, Weibull, log-normal, and log-logistic distributions are often used to model event data. Methods for finding the best fitting distribution are not canonized, varying with the distribution and type of censoring. A qualitative search for the appropriate distribution can be conducted by plotting event functions on probability paper. This renders the plot linear if the appropriate distribution is chosen (Nelson 1982). The adequacy of distributions can be gauged also by the magnitudes of their maximized log likelihoods (Kalbfleisch and Prentice 1980). Relative performance of two distributions, when one is a special case of the other (e.g. exponential and Weibull distributions), can be evaluated by a likelihood ratio test. We invoked all three procedures in our examples.

We adopted a two-step approach in the examples below. First, we fit the data to parametric models. Second, we evaluated treatments effects by testing for differences among parameter estimates for our experimental groups (example (1)) or estimating treatment effects and predicting event times for other, unobserved treatment values using a linear model (example (2)). This approach is general because familiar distributions often fit event times well, and linear models are suited for many null hypotheses of interest. However, other semi- and nonparametric approaches may be appropriate for any given data set (see examples in Gross and Clark (1975); Kalbfleisch and Prentice (1980); Lee (1980)).

Weibull Distribution

A Weibull distribution was selected to model event data in both our examples. This distribution has been used widely to describe event times since its first application in the analysis of material breaking strength (Weibull 1951). The Weibull invokes a power dependency of the hazard function on time. The exponential distribution is a special case of the Weibull and is widely used in fisheries to approximate mortality. Unfortunately, the constant hazard rate or "memory-less" property which makes the exponential easy to apply, also limits its appropriateness as a hazard function. For survivorship, a constant hazard implies invariant mortality rates with age and random (Poisson) deaths. There is little support for this assumption with respect to the timing of life history events.

The Weibull is a two-parameter distribution with hazard function,

$$(4)\quad h(t) = (\gamma/\alpha)\,(t/\alpha)^{\gamma-1}$$

where t, α, $\gamma > 0$. The scale parameter, α is in units of the event observations (e.g. days, weeks). It is often called the characteristic life parameter because its value is approximately equal to the 63rd percentile of the distribution. Some authors (e.g. Kalbfleisch and Prentice 1980; Lee 1980) parameterize the Weibull with the reciprocal of α as the scale parameter. The shape parameter, γ, is dimensionless. The survival function for the Weibull is

$$(5)\quad S(t) = \exp\left[-(t/\alpha)^{\gamma}\right] = 1 - F(t)$$

and the p.d.f. is

$$(6)\quad f(t) = (\gamma t^{\gamma-1}/\alpha^{\gamma}) \exp\left[-(t/\alpha)^{\gamma}\right] = dF(t)/dt$$

The Weibull is identical to the exponential distribution when $\gamma = 1$ and approaches the normal distribution when $3 < \gamma < 4$. It is an attractive descriptor of biological survival functions because it yields Deevey's (1947) Type I, II, or III survivorship curves when $\gamma > 1$, $= 1$, or < 1, respectively (Fig. 1A). A third parameter, τ, can be added to the Weibull to account for a threshold time below which Prob$[T] = 0$. It translocates the distribution by τ units so all functions are derived with $T - \tau$ as the observation.

Data analysis with a Weibull distribution usually enlists the natural log of event times, $Y_i = \ln(T_i)$. This transformation yields an extreme value distribution with parameters of location, β $(= \ln(\alpha))$, and scale, $\sigma(= \gamma^{-1})$. Such data are more easily treated because two or more distributions now have common shapes and are described by location and scale parameters, analogous to the mean and variance of a normal distribution. Parameters are estimated, event functions are evaluated, and then, using the exponential transformation, Weibull parameter estimates and evaluated functions are reported in the original units.

Series of event times can be compared by testing the equality of their Weibull parameter estimates. This is done in example (1). Regression models are a general method to evaluate the effects of covariables on event distributions. One model, the accelerated failure time model, is used in example (2) assuming a Weibull distribution of event times.

Accelerated Failure Time Model

Observations on additional variables are often recorded with event times. These variables may be quantitative or qualitative and represent planned treatments, environmental covariables, or subject attributes. These k variables, described by the vector, $\mathbf{v}' = (v_1, v_2, \ldots, v_k)$, are used as explanatory variables. Assuming that the elements of $\mathbf{v}$ interact through a linear function, $\mathbf{v}'\boldsymbol{\beta}$, the parameters, β_i's, are estimated for the corresponding explanatory variables. The β_i's are useful in two ways: (1) to evaluate the hypothesis $\beta_i = 0$ (i.e. the explanatory variable v_i has no effect) and (2) to predict events at other values of the explanatory variable if $\beta_i \neq 0$, as in regression analysis.

The event functions, equations (1–3), are modified to include these additional components. Using the hazard function, $h(t)$, the modification leaves $h(t)$ conditional on the explanatory variables,

$$(7)\quad h(t;\mathbf{v}) = hc(\mathbf{v}'\boldsymbol{\beta})$$

where c is usually specified as the exponential function, $exp(\cdot)$ (Kalbfleisch and Prentice 1980). For the Weibull hazard function, equation (4), the conditional hazard of equation (7) becomes,

$$(8)\quad h(t;\mathbf{v}) = (\gamma/\alpha)(t/\alpha)^{\gamma-1} \exp(\mathbf{v}'\boldsymbol{\beta})$$

Using equation (A1.6; see appendix 1), the conditional survival function is

$$(9)\quad S(t;\mathbf{v}) = \exp\left[-(t/\alpha)^{\gamma} e^{\mathbf{v}'\boldsymbol{\beta}}\right]$$

Applying equation (A1.7; appendix 1), equations (8) and (9) yield the conditional density for the Weibull distribution,

$$(10)\quad f(t;\mathbf{v}) = (\gamma t^{\gamma-1}/\alpha^{\gamma})\, e^{\mathbf{v}'\boldsymbol{\beta}} \exp\left[-(t/\alpha)^{\gamma} e^{\mathbf{v}'\boldsymbol{\beta}}\right]$$

Observations of event times usually are related to the explanatory variables as,

$$(11)\quad \mathbf{Y} = \mathbf{V}\boldsymbol{\beta} + \sigma\boldsymbol{\epsilon}$$

where $\mathbf{Y}$ is the vector of log event times, $\mathbf{V}$ is the matrix of explanatory variables, $\boldsymbol{\beta}$ is the vector of coefficients to be estimated, σ is the scale parameter to be estimated, and $\boldsymbol{\epsilon}$ a random vector from an assumed distribution (e.g. the extreme value distribution). The first column of $\mathbf{V}$ is typically a unit vector such that β_1 estimates the intercept which in this context is the location parameter of the extreme value distribution (i.e. $\beta_1 = \beta = \ln(\alpha)$). The estimated scale parameter of the extreme value distribution equals the inverse of the Weibull shape parameter. Equation (11) is framed so that explanatory variables act additively on Y or, due to the log transformation, multiplicatively on T, leading to an acceleration or deceleration of event times; hence the name accelerated failure time models.

Solutions to Event Time Models

The maximum likelihood (m.l.) method is the preferred way to estimate parameters of an event time distribution and regression model (β_1, β_2,..., σ), because it allows analyses of complete data and series with single and multiply censored observations. Under broad conditions m.l. estimators are consistent and asymptotically normally distributed, efficient (i.e. possess minimal sampling variance), and unbiased (Kendall and Stuart 1979; see Cohen and Whitten (1988) for limitations vis-à-vis event analysis). Solutions to the likelihood equations are usually solved iteratively (appendix 2).

Examples

(1.) Age at Metamorphosis — Parental Effects

Here we analyze metamorphosis timing in winter flounder (*Pseudopleuronectes americanus*). We (1) fit the Weibull to the distribution of age at metamorphosis of fish from two sets of parents, (2) test the null hypothesis of no differences between scale or shape parameters for the two full-sibling sets, and (3) calculate the effects of family differences in metamorphosis timing on survival in a hypothetical temporary habitat. We use data on two full-sibling families from a larger study of age and size at metamorphosis of laboratory-reared winter flounder (Chambers and Leggett 1987). Our analysis is based on observations pooled from three replicate aquaria for each family. Not all larvae had metamorphosed by the end of the rearing period, therefore these data contain right-censored observations.

Methods

Ripe winter flounder were collected from Bryants Cove and Harbor Grace, Newfoundland by gill netting and SCUBA in May 1986. Adults were artificially mated and zygotes were transferred to a water bath maintained at 5°C. At 1 to 3 d prior to hatching three sets of 400 late-eyed embryos from each family were placed into 38-L glass aquaria and reared as full-sibling groups. Rearing conditions were static except for partial water replacement of about 250 mL at food additions every 1–2 d. Larvae were fed in excess with laboratory-cultured rotifers (*Brachionus*), *Artemia*, and natural zooplankton from local waters. Chilled water baths kept all rearing aquaria at 7 ± 0.8°C (mean ± SD) and 16 h:8 h light regime was maintained. Methodological details are in Chambers and Leggett (1987).

Aquaria were checked daily as metamorphosis approached. Metamorphosis was defined as the point at which the iris of the migrating eye was visible from the right side of the body. This is equivalent to stage 5 of Shelbourne (1957) and Ryland (1966) and stage H of Seikai et al. (1986). Individuals satisfying this criterion were transferred to new aquaria holding only juveniles. Age at metamorphosis was defined as days between the day on which an individual fish was scored as a juvenile and the modal hatching day for larvae from its aquarium.

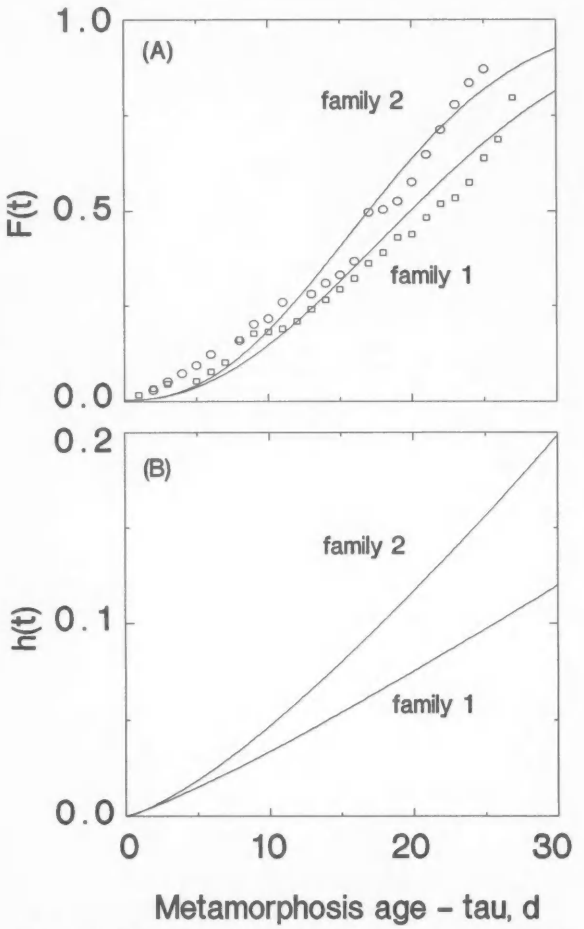

FIG. 2. (A) Observed (□, ○) and estimated (—) ages at metamorphosis in two families of laboratory-reared winter flounder expressed as cumulative distributions, $F(t)$. Ages at metamorphosis were shifted by $\tau = 44$ d prior to fitting. Observed values were reduced from event records (Table 1) using the product-limit estimator, $F(t) = 1 - \prod_{i|t_i < t} (r_i - n_i)/r_i$, where r_i and n_i are, respectively, the total number at risk of undergoing the event and the number of events observed at age i. Parameter estimates for fitted Weibull distributions are based on observed and censored events (Table 1). (B) Age-specific metamorphosis rate (hazard function, $h(t)$) for the Weibull distributions in (A).

Results and discussion

The distribution of age at metamorphosis was described by a Weibull distribution for each family (Fig. 2A). Parameter estimates and 95% confidence limits (Table 1) were calculated using a threshold parameter of $\tau = 44$ d set by the minimum observed age at metamorphosis among all reared populations

TABLE 1. Event data and parameter estimates for examples given in text. Estimates of scale and shape parameters (95% confidence limits) are given for Weibull distributions. Age at metamorphosis for two families of winter flounder was shifted by $\tau = 44$ d before fitting. Censored observations were entered on the last day metamorphosis was observed for each family (*). Age at death for unfed capelin hatchlings maintained at 6, 9, and 12°C is in days since hatching. All observations were log transformed prior to analysis.

	Number observed				
	Metamorphosis		Death		
Day observed	Family 1	Family 2	6°	9°	12°
1	4				1
2	4	4			
3	3	3			2
4		3			
5	2	3		1	1
6	6	4			1
7	6			1	4
8	15	5			4
9	4	6	1	3	5
10	1	2		3	6
11	2	6		2	1
12	5		1	8	
13	8	3		2	
14	6	4	4	3	
15	7	3	5	1	
16	7	5	5	1	
17	10	18	6		
18	7	1	1		
19	10	3	1		
20	2	7			
21	11	10	1		
22	9	9			
23	4	9			
24	10	8			
25	16	5*			
26	12				
27	27*				
No. observed	198	121	25	25	25
No. censored	51	18	0	0	0
Scale, α	23.6 (22.1–25.2)	19.9 (18.4–21.5)	16.6 (15.8–17.5)	12.4 (11.5–13.3)	8.5 (7.7–9.5)
Shape, γ	2.1 (1.9–2.4)	2.3 (2.0–2.7)	7.7 (6.0–10.8)	5.6 (4.3–8.1)	3.8 (2.8–5.7)

(18 populations, 662 individuals, Chambers and Leggett (1987)). The Weibull proved superior to the log-normal and log-logistic by both graphical and maximized log-likelihood criteria and provided a better fit than the exponential (likelihood ratio test, $\chi_1^2 = 109.6$, $p<0.001$ and $\chi_1^2 = 80.4$, $p<0.001$, for family 1 and 2, respectively). Age-specific probability of metamorphosis increased with age for each family (Fig. 2B).

Family differences in age at metamorphosis were evaluated with a likelihood ratio test wherein the hypothesis of no difference between shape and scale parameters of age at metamorphosis ($\alpha_1 = \alpha_2$ and $\beta_1 = \beta_2$) was tested (Nelson 1982; p. 538). Families differed significantly by this criterion ($\chi_2^2 = 11.1$; $p<0.005$). These differences appeared due to a shift of the distribution between the two families (Table 1, Fig. 2). Because the fit of the Weibull for each family was short of ideal, we further tested the null hypothesis of no family difference by a nonparametric log-rank test (Kalbfleisch and Prentice 1980). This test corroborated our result from Weibull parameters (Mantel test: $\chi_1^2 = 21.12$, $p<0.001$).

Next we evaluated the potential survival consequence in a hypothetical temporary habitat of the observed difference between the two families in their ages at metamorphosis. The range in age at metamorphosis was >35 d in these populations (Chambers and Leggett 1987). We asked the question: what fraction of each family will metamorphose by a predetermined day into the time interval during which metamorphosis was observed for all populations? We arbitrarily picked 21 d for an example — another duration would result in a quantitatively different conclusion. We used this time to represent an environmentally induced truncation of the right side of the distribution of age at metamorphosis. Reported occurrence of good and poor food patches for larvae (Shelbourne 1957) and degradation of thermal environments suitable for high prey concentration (Lasker 1975) in nature support our question, although this scenario probably varies among populations, years, etc. Using parameter estimates for each family (Table 1) and the expression for the c.d.f. of the Weibull, equation (5), we find that

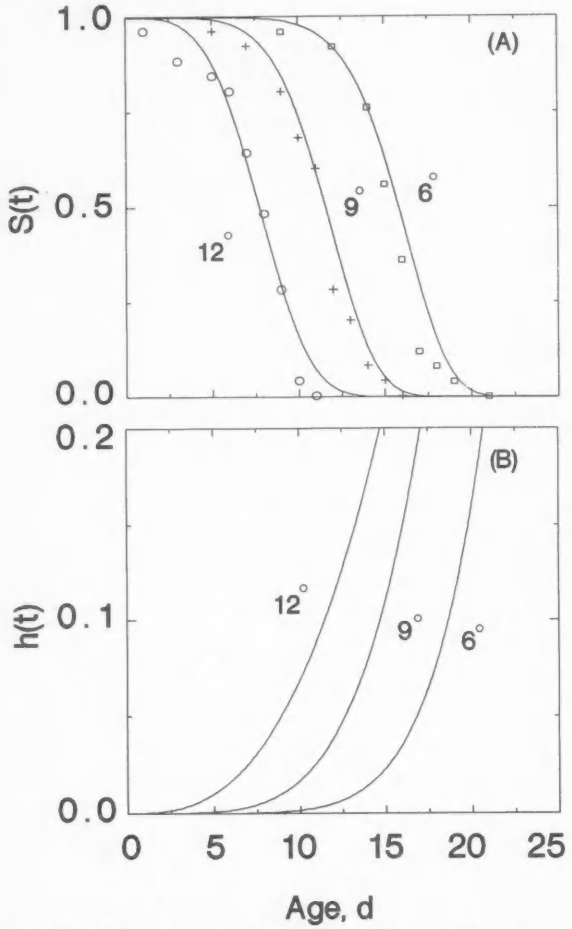

FIG. 3. (A) Observed (□, +, ○) and estimated (—) survival functions, $S(t)$, of unfed capelin hatchlings maintained at 6, 9, and 12°C. Observed values were generated from event records (Table 1) using the product-limit estimator (Fig. 2). Parameter estimates for fitted Weibull distributions are in Table 1. (B) Age-specific mortality rate (hazard function, $h(t)$) for the Weibull distributions in (A).

$$(12)\quad \hat{F}_1(21) = 1 - S(21) = 1 - \exp[-(21/23.62)^{2.15}] = 0.54$$

and,

$$\hat{F}_2(21) = 1 - S(21) = 1 - \exp[-(21/19.91)^{2.31}] = 0.68,$$

where $\hat{F}_i(21)$ is the estimated c.d.f. through 21 d for family i. The approximate 95% confidence limits (Nelson 1982) for families 1 and 2 are (0.49, 0.59) and (0.61, 0.74), respectively.

These calculations show that the number of individuals of family 2 which successfully enter the juvenile period within our 21-d time constraint is about 25% greater than those of family 1. This hypothetical example emphasizes the potential of event analysis to (1) discriminate those fish which are most likely to successfully exit the larval period and (2) predict their relative abundances. This knowledge could be used to refine estimates of recruitment and to improve production or broodstock in the controlled culturing of fishes where life history events monitored are traits of interest or are correlated with such traits.

TABLE 2. Parameter estimates and test of temperature effects on age at death for unfed capelin hatchlings using the accelerated failure time model, equation (11), with log-transformed observations. The X^2 statistic tests the null hypothesis of no temperature effect (i.e. $\beta_2 = 0$) with $df = 1$. The variance = covariance matrix of parameter estimates, Σ, is used in equation (15) to estimate confidence limits for percentiles of the cumulative age-at-death distribution.

Parameter	Estimate	SE	X^2	$p<$	$\Sigma \times 10^3$		
					β_1	β_2	σ
Location, β_1	3.42	0.085			7.18	−0.74	−0.02
Temperature, β_2	−0.10	0.009	129	0.001		0.08	−0.01
Scale, σ	0.19	0.018					0.32

(2.) Survival of Yolk-Sac Larvae — Temperature Effects

Here we analyze the lifespan of unfed capelin (*Mallotus villosus*) hatchlings. We (1) fit the Weibull to age-at-death data for larvae held at three constant temperatures, (2) test the null hypothesis of no temperature effect on posthatching survival using an accelerated failure time model, and (3) predict percentiles of the expected survival function at an untested temperature by employing the estimated failure time model. We use data from a study of phenotypic variation in capelin early life history traits (R. C. Chambers et al., unpubl. data). Larvae were from four different parental sets. We analyzed 25 larvae at each temperature. Hence, in this example the data are complete (i.e. no censoring).

Methods

Ripe capelin were collected from a beach spawning population in Bryants Cove, Newfoundland in June 1986. Adults were artificially mated and zygotes transferred to a water bath maintained at 7 ± 0.8°C. After 2 d each of 45 viable zygotes/female was placed into its own 36-mL glass shell vial. Each vial was filled to 30 mL with filtered (0.45 μm) seawater. Fifteen vials from each female were transferred to water baths maintained, nominally, at 6, 9, or 12°C. Seawater in the vials was replaced every 2 d until hatching commenced. Vials were checked daily to record the day of hatching and day of death of each of these unfed larvae. Age at death was the difference between these two records.

Results and discussion

The distribution of age at death for each temperature was described by a Weibull distribution (Fig. 3A). Parameter estimates and 95% confidence limits (Table 1) were calculated with the threshold parameter, τ, set to zero (i.e. age at starvation is days since hatching). The Weibull fit the age-at-death series better than did the log-normal or log-logistic based on graphical and optimization criteria and was superior to the exponential distribution at all temperatures ($X_1^2 = 75.7$, 58.0, and 38.5 for 6, 9, and 12°C, respectively; $p < 0.001$ for all tests). Age-specific mortality increased with age at each temperature (Fig. 3B and as documented by the γ's > 1 (Table 1)).

As expected, and often reported (Blaxter 1988), age at starvation increased significantly as temperature decreased (Table 1, Fig. 3). The inverse action of temperature on age at starvation is reflected by the accelerated failure time model where $\beta_2 < 0$ (Table 2).

We next used the accelerated failure time model to predict percentiles of the age-at-death distribution of capelin hatchlings at an unobserved temperature. For demonstration, we made three assumptions. First, prey are patchily distributed. Second,

water temperature experienced by these larvae averages 10.5°C and the effect of temperature fluctuations about this average can be ignored. Third, a precondition for good versus poor year-classes of capelin is that >50% versus <25% of yolk-sac larvae survive until a sufficiently dense concentration of edible zooplankton is encountered. The problem can be stated in two parts as follows: (1) how many days does this cohort have to encounter a food patch and still produce a large year-class, and (2) after how many days without encountering a food patch will this cohort be rendered a poor year-class?

We answered this question by estimating the 50th and 75th percentiles of the c.d.f. for age-at-death. We used the parameter estimates, variances, and covariances from the accelerated failure time model (Table 2). The 100 Pth percentile of the extreme value distribution is

$$(13) \quad y_P = \beta_1 + u_p\sigma,$$

where $y = \ln(t)$, β_1 and σ are estimated location and scale parameters, respectively, of the extreme value distribution and $u = \ln[-\ln(1-P)]$ is the 100 Pth standard extreme value percentile. The temperature covariable, v, and its coefficient, β_2, contribute additively to equation (13) to yield,

$$(14) \quad y_P = \beta_1 + v\beta_2 + u_P\,\sigma$$

The estimated 50th percentile at 10.5°C is,

$$\hat{y}_{0.5} = 3.42 + (10.5)(-0.10) + (-0.37)(0.19) = 2.27.$$

The 95% confidence limits of $\hat{y}_{0.5}$ are estimated by ± 1.96 $(\mathrm{Var}[y_{0.5}])^{0.5}$ where $\mathrm{Var}[y_P]$ is calculated as,

$$(15) \quad (1, \bar{T}, u_P)\ \Sigma\ (1, \bar{T}, u_P)'$$

with $\bar{T}$ the mean temperature, u_P the 100 Pth percentile of the standard extreme value distribution, and Σ the variance–covariance matrix for the parameter estimates (Table 2). The 95% confidence limits for $y_{0.50}$ are ± 0.05. Transforming these estimates back to the original units by $\exp[y_i]$ reveals that the cohort has 9.66 d (95% C.L.:9.21, 10.14) to encounter a food patch and still maintain the potential of generating a good year-class. The calculation for the 75th percentile (i.e. 25% of the larvae still alive) yields $\hat{y}_{0.75} = 2.40 \pm 0.04$. Therefore, in this example a poor year-class would result if a food patch is not encountered within 11.01 d (95% C.L.:10.58, 11.45).

This example shows how the magnitude of effects due to changes in an environmental covariable, coupled with an explicit recognition that events are distributed in time, can be used to predict the abundance of larvae. This example clearly illustrates the precariousness of survival in the early larval period, and its potential for affecting recruitment. In this case the larval population was halved and the opportunity lost for generating a strong year-class within 1.5 d.

Translating this application of event analysis to natural populations would require further adjustments. For example, the average temperature experienced by larvae probably influences the preconditions for establishment of year-class quality because the leeway between exhaustion of yolk reserves and successful establishment of exogeneous feeding varies with temperature (see for example, Buckley (1982)). Moreover, in nature, other sources of mortality act. In theory, the effects of explanatory variables on these separate sources of mortality can be estimated with competing risks models (Kalbfleisch and Prentice 1980), but this may require data of a resolution difficult to obtain for natural populations. Nevertheless, Leggett et al. (1984) provide evidence that temperatures in the earliest portion of the larval period are important to capelin survival and can be used to predict year-class strength 2 yr later. The mechanism they suggest differs from that evaluated here, but their result supports the potential importance of small changes in easily monitored environmental covariables to early life history events.

Conclusions

We have applied event analysis to ontogenetic timing in marine fishes. These techniques have three immediate advantages. (1) Information from all observations, including censored ones, contributes to the analysis, allowing more complete and less biased use of data. (2) Event schedules can be rigourously compared between groups. (3) Regression models can assess the role of covariables on, and predict timing of these events.

Event analysis requires time-at-event observations on individuals. Such observations are often made on laboratory fish or in aquacultural systems, so the described methods are easily applied there. No restrictions apply to the kind of event measures; life history events (e.g. hatching, yold-sac depletion, first feeding, metamorphosis, smoltification, maturation, spawning, and death), ecological events (e.g. habitat, diet, and behavioural mode shifts), and responses to experimental challenges can all be treated. Measurement of these events is more difficult, yet more realistic, in natural populations. Some life history events of individuals in natural populations are now recoverable through their record on otolith structure (e.g. Penny and Evans 1985; Rice et al. 1987).

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Appendix 1

As defined by equation (2′), $f(t)$ is the p.d.f. of event times, therefore,

$$\text{(A1.1)} \quad \int_0^t f(x)dx = F(t) = 1 - S(t)$$

or,

$$\text{(A1.2)} \quad f(t) = \frac{dF(t)}{dt} = \frac{d[1 - S(t)]}{dt}$$

so the p.d.f. in terms of the survival function is,

$$\text{(A1.3)} \quad f(t) = -\frac{dS(t)}{dt}$$

The hazard function, conditional on survival to time t, is related to $f(t)$ and $S(t)$ by,

$$\text{(A1.4)} \quad h(t) = \frac{f(t)}{S(t)}$$

Substituting equation (A1.3) into equation (A1.4) gives $h(t)$ in terms of $S(t)$,

$$\text{(A1.5)} \quad h(t) = -\frac{dS(t)/dt}{S(t)} = -\frac{d[\ln S(t)]}{dt}$$

Integrating equation (A1.5) and recognizing that $S(0) = 1$ leaves,

$$-\int_0^t h(x)dx = \ln S(t)$$

$S(t)$ defined in terms of the $h(t)$ is, therefore,

$$\text{(A1.6)}\quad S(t)=\exp\left[-\int_0^t h(x)dx\right]$$

Rearranging equation (A1.4) and using equation (A1.6) leaves $f(t)$ in terms of $h(t)$,

$$\text{(A1.7)}\quad f(t)=h(t)\exp\left[-\int_0^t h(x)dx\right]$$

Appendix 2

The maximum likelihood method can be applied to the event functions for estimating parameters once a baseline distribution has been specified. The method is demonstrated for the two-parameter Weibull distribution with censored data, although it can be generalized to p parameters. Complete data are a special case of the censored situation. Further details are in Mann et al. (1974) and Nelson (1982).

Let a set of observations be denoted by $(T_1, T_2, \ldots, T_e, T_e+1, \ldots, T_{e+c})$ with e events and c censored observations. For a set of $n=e+c$ observations from a distribution with $f(\cdot)$ and $S(\cdot)$ as the p.d.f. and survival function, respectively, the sample likelihood $L(z)$ for parameters $z' = (\alpha, \gamma)$ is defined as,

$$L(z) = f(T_1; z)\times\ldots\times f(T_e; z)\times S(T_{e+1}; z)\times\ldots\times S(T_{e+c}; z)$$

$$= \prod_{i=1}^{e} f(T_i; z)\times \prod_{i=e+1}^{e+c} S(T_i; z)$$

The natural log of this product is the sample log-likelihood,

$$\text{(A2.1)}\quad \mathcal{L}(z)= \sum_{i=1}^{e} f(T_i; z)+ \sum_{i=e+1}^{e+c} S(T_i; z).$$

The m.l. estimate of z is the value that maximizes $\mathcal{L}(z)$. This value is found by setting partial derivatives for each parameter, z_i, equal to zero and solving for $\hat{z}_i$,

$$\text{(A2.2)}\quad \partial\mathcal{L}(z_i)/\partial z_i=0 \qquad \text{for } i=1 \text{ to } p.$$

To estimate the scale and shape parameters of the Weibull distribution, first $f(t)$, equation (10), and $S(t)$, equation (9), are used in equation (A2.1). The resulting log likelihood is,

$$\text{(A2.3)}\quad \mathcal{L}(\alpha,\gamma)= \sum_{1}^{e} [\ln(\gamma)+(\gamma-1)\ln(T_i)-\gamma\ln(\alpha) - (T_i/\alpha)^{\gamma}] + \sum_{e+1}^{e+c} [-(T_i/\alpha)^{\gamma}].$$

Then the m.l. estimates, $\hat{\alpha}$ and $\hat{\gamma}$, are found by solving the following system of equations:

$$\text{(A2.4)}\quad \partial\mathcal{L}/\partial\alpha= \sum_{1}^{e}[-(\gamma/\alpha)+(\gamma/\alpha)(T_i/\alpha)^{\gamma}]+ \sum_{e+1}^{e+c} (\gamma/\alpha)(T_i/\alpha)^{\gamma}=0$$

$$\partial\mathcal{L}/\partial\gamma= \sum_{1}^{e} [(1/\gamma)+\ln(T_i/\alpha)-(T_i/\alpha)^{\gamma}\ln(T_i/\alpha)]$$

$$- \sum_{e+1}^{e+c} (T_i/\alpha)^{\gamma}\ln(T_i/\alpha)=0.$$

Alternatively, the observations are log transformed to yield an extreme value distribution. The equations for this distribution, analogous to equations (A2.3) and (A2.4) are,

$$\text{(A2.3')}\quad \mathcal{L}(\beta,\sigma)= \sum_{1}^{e} \{-\ln(\sigma)-\exp[(Y_i-\beta)/\sigma] + [(Y_i-\beta)/\sigma]\} - \sum_{e+1}^{e+c} \exp[(Y_i-\beta)/\sigma]$$

and

$$\text{(A2.4')}\quad \partial\mathcal{L}/\partial\beta=(1/\sigma)\left[\sum_{1}^{e+c} \exp((Y_i-\beta)/\sigma)-e\right]=0$$

$$\partial\mathcal{L}/\partial\sigma=(1/\sigma)\left[\sum_{1}^{e+c} ((Y_i-\beta)/\sigma)\exp((Y_i-\beta)/\sigma) - \sum_{1}^{e} ((Y_i-\beta)/\sigma)-e\right]=0,$$

where $Y_i=\ln(T_i)$, $\beta=\ln(\alpha)$, and $\sigma=\gamma^{-1}$. These nonlinear likelihood equations, (A2.4) or (A2.4'), are solved iteratively. A commonly used method, the Newton–Raphson, is used here (Nelson 1982). Through estimation of the parameters this method genrates, and evaluates at $\hat{z}$, the observed information matrix used to estimate their standard errors. Several statistical packages contain survival analyses that provide estimates of parameters and their asymptotic standard errors (e.g. SAS Institute Inc. 1987; Steinberg and Colla 1988).

Larval Mosquitoes as Vulnerable Prey: *Chaoborus* Predation[1]

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Helgen, J. C. 1989. Larval mosquitoes as vulnerable prey: *Chaoborus* predation. Can. J. Fish. Aquat. Sci. 46: 1642–1650.

The vulnerability of instar I and II larvae of the mosquito *Aedes vexans* as prey for *Chaoborus americanus* is much greater than that of the small coexisting prey, *Daphnia pulex*. Predation on *Aedes* larvae could reduce *Aedes* populations in overlapping habitats, and be a selective force in driving *Aedes* to lay eggs in muds of more temporary wetlands. Predation rates are great (7–25·d^{-1}) and ingestion times are rapid (0.8–6 s) on *Aedes* instars I and II. In prey choice experiments, *Chaoborus* strongly prefers *Aedes* I over small *Daphnia*. An *Aedes* diet promotes growth of *Chaoborus* at least as well as a *Daphnia* diet. Larval *Aedes* behaviors show a distinct difference between the first two and last two instars. *Aedes* swimming speeds and swimming distances increase with each instar, but when disturbed, the first two instars significantly reduce their swimming distances. Calculated prey vulnerabilities, based on swimming speeds and reciprocal ingestion times, suggest a much greater vulnerability for *Aedes* I and II than that for small (0.8 mm) *Daphnia* or for *Aedes* III and IV (4.6–6.2 mm).

Les stades larvaires I et II du moustique *Aedes vexans* sont beaucoup plus vulnérables à la prédation par *Chaoborus americanus* que *Daphnia pulex*, une autre petite proie de *C. americanus* qui vit dans le même milieu qu'*A. vexans*. Les populations d'*Aedes* peuvent diminuer à cause de la prédation dans les habitats où les larves de cet insecte cohabitent avec *C. americanus*; cette prédation peut donc agir comme une pression de sélection et incite les femelles d'*Aedes* à déposer leurs oeufs dans la boue ou dans des milieux humides plus temporaires. Le taux de prédation des stades larvaires I et II d'*Aedes* sont élevés (7–25 j^{-1}) et les durées d'ingestion sont courts (0,8–6 s). Des expériences de choix de proies ont montré que *Chaoborus* préférait de beaucoup les larves d'*Aedes* du stade I aux petites *Daphnia*. Les *Chaoborus* nourris d'*Aedes* ont une croissance aussi bonne sinon meilleure que quand ils sont soumis à un régime de *Daphnia*. Par ailleurs, les comportements des larves d'*Aedes* des deux premiers stades larvaires sont nettement différents des comportements de celles de ses deux derniers stades larvaires. Les larves d'*Aedes* nagent de plus en plus rapidement et sur de plus longues distances à chaque nouveau stade larvaire, mais les larves des deux premiers stades larvaires diminuent sensiblement leurs distances de déplacement quand leur environnement est perturbé. Des calculs de vulnérabilité à la prédation fondés sur les vitesses de nage et les durées d'ingestion semblent indiquer que les larves des stades larvaires I et II d'*Aedes* sont beaucoup plus vulnérables que les petites (0,8 mm) *Daphnia* ou les larves des stades larvaires III et VI d'*Aedes* (4,6–6,2 mm).

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Very little is known of the potentially important prey–predator relationship between larval mosquitoes and the predatory larvae of the midge *Chaoborus americanus*, often found in shallow fishless ponds (von Ende 1978). Because the eggs of the common mosquito *Aedes vexans* are laid in the wet muds of retreating margins of shallow semi-permanent or permanent wetlands, newly hatched *Aedes* larvae will be exposed to predation by overwintering *Chaoborus* larvae as the ponds refill from snow-melt and spring rains. As water floods back over marginal egg-bearing muds, the hatch of *Aedes* eggs is triggered by an oxygen drop, and the subsequent development rates are strongly temperature driven (Horsfall et al. 1973).

Although the predatory activities of *Chaoborus* larvae on zooplankton have been well analyzed (Fedorenko 1975; Giguere and Dill 1979; Havel and Dodson 1984; Moore 1986; Neill 1981; Pastorak 1981; Reissen et al. 1984; Swift and Fedorenko 1975; Vinyard and Menger 1980), quantitative reports of *Chaoborus* predation on mosquito larvae are meager. Reports include a consumption rate of 0.6 *Aedes* per day by *C. americanus*, consumption of *Aedes* pupae by *C. nyblaei* (James and Smith 1958), an observation of nine instar I *Aedes* eaten by one *Chaoborus* in a day, and a lack of *Aedes* in ponds with abundant *Chaoborus flavicans* (Sailer and Lienk 1954). There are no other reports on measured predation rates and none on prey density effects, prey preference tests including mosquito larvae, or handling times for *Chaoborus* consuming mosquito larvae.

This paper presents research in two relatively unexplored areas: first, the potential for impact by *Chaoborus* predation on mosquito larvae, and second, stage-specific behaviors of larval *Aedes vexans* that might affect their vulnerability to predators. Data are given on predation rates by *Chaoborus americanus* on all four instars of *Aedes vexans*, effects of prey density on the functional response, ingestion times for each *Aedes* instar consumed, and strike efficiencies on first instar *Aedes* by *Chaoborus*. *Chaoborus* predation on mosquito larvae is compared with that on the cladoceran *Daphnia pulex* because of the documented success of the latter species to maintain populations

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in the presence of *Chaoborus* predation pressures (Havel and Dodson 1984; Havel 1985). *Chaoborus* preference for *Aedes* instar I over *Daphnia pulex* juveniles is demonstrated by prey choice experiments. To explore whether *Aedes* is a profitable prey for *Chaoborus*, data are given on growth rates and time to pupation on both *Daphnia* and *Aedes* diets at two temperatures. A relative vulnerability for each of the four instars of *Aedes* is calculated using swimming speeds and reciprocal ingestion times, and then compared with estimated relative vulnerabilities for *Daphnia*. Finally, results of timed larval mosquito behaviors that might affect vulnerability to predation, such as swimming speeds and swimming distances, with and without a disturbance, are given for each instar.

Methods

Mosquito Methods and Growth

Eggs of *Aedes vexans* were collected from April to June in the top 2 cm of soil at designated sites in a wooded temporary pond in the Crow Hassan Park Reserve, Hennepin County, MN. Soil samples with eggs were stored moist at 10°C in the dark until needed. For most egg hatches, 2–3 cm of soil were placed in plastic trays, which were filled with deionized water. Plastic wrap laid directly on the water surface to allow the O_2 depletion necessary for a successful hatch to occur was removed in 12–16 h, when a range of 50–250 young instar I larvae would be present.

Within 24 h of hatching, larval mosquitoes were either used for experiments as instar I, or were reared in white enamel pans with yeast as food to the desired stage. Predictions for development times at the two temperatures used, 18° and 26°C, were based on a predictive computer model (N. Read, Entomology Department, University of Minnesota, St. Paul, MN, in prep). This model predicted that the times in hours to the median instars, i.e. 50% at the instar, for 17.8°C would be 4.1 h for I, 72 for II, 124 for III, 180 for IV, and 292 for pupa, respectively. For 25.8°C, time in hours would be 4.1 for I, 40.1 for II, 60 for III, 88.1 for IV, and 136 for pupa, respectively.

An alternative method of egg hatching, used for the mosquito growth measurements, began with isolation of the eggs by flotation in 35% sucrose from soil previously sieved to retention on a 63 μm brass sieve. A variety of eggs, including both those of *Aedes* and cladoceran ephippia, can be isolated this way. After rinsing twice, the eggs showed the most successful hatch (80 or 100% in 2 h) when stored overnight in deionized water and then placed in screw-capped vials containing a 1:200 dilution of sterile trypticase-soy broth with a small amount of dry yeast added.

Mosquito growth rates were measured at 18 and 26°C by incubating 12 isolated individuals of known hatching time from eggs isolated by sucrose float and hatched in trypticase-soy broth. The larvae were fed yeast and the body length and head capsule width were measured daily. To see if temperature affected either body length or head capsule width, Student's *t* tests were performed for each of the four instars at the two temperatures. Dry weights were determined on 10 instar IV individuals and on three sets of 30 measured pooled instar I larvae dried at 60°C 24 h and weighed three times with a 6-place Mettler Micro-Gramatic balance.

Chaoborus Experiments

Chaoborus americanus larvae obtained from a semi-permanent seepage pond in the Crow Hassan Park Reserve from April through June were kept at 4°C in the dark until needed. Measurements were made of body length, head length, and mouth gape. The gape measurement was made of the width of the base of the mandibles at the widest point when viewed ventrally, head capsule length was made in lateral view.

To test the effectiveness of a mosquito diet for *Chaoborus*, instar III and IV *Chaoborus* larvae were grown until pupation at 18 and 26°C on a daily diet of either 10–15 juvenile *Daphnia pulex*, a known prey species, or 10–15 instar I *Aedes* larvae. *Daphnia pulex* were collected from the *Chaoborus* pond, and reared continuously with a yeast diet in the lab. "Juvenile" *Daphnia* were prereproductive, their size averaging 0.76 mm. *Chaoborus* body length (at 20×) and head length (at 80×) were measured weekly. Results are reported as growth increments (in millimetres) from the initiation of the experiment to just prior to pupation. *Chaoborus* III and IV were selected so the initial sizes of the four groups (two temperatures, two diets) were not significantly different. Student's *t* tests were performed on the differences between the means of the growth increments and times to pupation with the two diets at the two temperatures.

Chaoborus densities for the pond of origin for an earlier year with instars by percent are given. Densities are based on weekly triplicate plankton tows across a defined distance using a pontoon-mounted Wisconsin plankton net (see Helgen et al. 1988).

Predation Experiments

Ten predation experiments at 18 and 26°C using III and IV instar *Chaoborus* larvae and the four larval instars of *Aedes vexans* and *Daphnia* juveniles as prey were carried out. The experiments were run with one *Chaoborus* per jar with 750 mL temperature-conditioned, aged water at 18 or 26°C. From five to 12 *Chaoborus* were tested in each of the trials, with *Aedes* instars I, II, and IV, and from three to seven with *Aedes* III. Controls without *Chaoborus* were always run as checks on prey mortality. Experiments began around 1600–1700 h and ended around 0900–1000 h for intervals of 16–17 h. The light cycle was 16L:8D, off at 2200, on at 0600 h. *Chaoborus* and prey were preserved for later measurement.

A functional response experiment to see how predation rate varied with prey density was carried out for 2 h at 21–22°C under fluorescent lights with six *Chaoborus*, one per 750-mL jar, at each *Aedes* density tested. Densities tested were 1, 6, 12, 24, and 48 *Aedes* per 750 mL for instars I, II, and III, with no 48 level for instar IV.

Ingestion times by *Chaoborus* for each of the *Aedes* instars were observed on 7–13 *Chaoborus* consuming *Aedes* instars I, II, and III, and on two consuming instar IV. Ingestion time was the time from initial capture to complete ingestion of the larvae. Observations were made using a light box at room temperature, 21–22°C. Strike efficiencies were measured two times, one on seven, the second on 10 *Chaoborus* presented instar I *Aedes*. A successful strike was recorded as a capture, an unsuccessful attack that resulted in no capture as a miss.

In prey choice experiments, *Chaoborus* were presented with equal numbers of *Daphnia* and instar I *Aedes* (M_I). One experiment was run 17 h at 26°C with 20 M_I and 20 juvenile *Daphnia* per 750 mL with one instar IV *Chaoborus* per jar, 11 *Chaoborus* jars and one control. The rest of the experiments were run with one *Chaoborus* IV for 2 h at 21–22°C in 120 mL with one juvenile *Daphnia* and one *Aedes* with replacement of prey as consumed.

Larval Mosquito Behaviors

To understand behaviors of *Aedes* larvae that might make them vulnerable to different types of predators during development, two groups of behaviors were observed. The first group of behaviors, such as wiggling or suspending, could expose the larva to a predator. The second behavior group, swimming speed and distance, relates to potential escape responses or encounter probabilities by the larvae. For the first group, a variety of behaviors by all four larval instars were observed and voice-recorded for 10-min intervals as seconds per behavior. Six to seven individuals of instars I, II, and IV, and four for instar III were observed. Behaviors recorded were:

(1) Wiggle (W); the thrashing, flipping swimming style of the mosquito larva,
(2) suspend cruise (SC); an even swimming motion driven by the mouth parts while the larva is suspended with the respiratory siphon at the surface, usually in a forward direction, sometimes spiralling,
(3) browse (B); the browsing feeding action of the mouth parts over the substrate, which causes the larva to move like a self-propelled vacuum cleaner (also called "brush" feeding),
(4) suspend (S); the larva hangs immobile from the surface by the respiratory siphon,
(5) suspend at bottom (SB); hanging motionless, siphon up, but close to the bottom.

All behaviors were recorded on isolated individuals at ambient room temperature (21–22°C) under overhead fluorescent lights in 23 × 15-cm plastic containers with 4-cm water depth. No predators were present.

One way ANOVA with comparisons of instars I and II with instars III and IV for the five behaviors was carried out (SPSS-X Release 2.1 for Vax Unix), because it appeared the behavior of the first two instars differed from III and IV, that is I and II responded to a disturbance in a manner entirely different from III and IV. One way ANOVA with a split-plot design was done to compare "active" (W, SC, B) with "inactive" (S, SB) behaviors for all four *Aedes* instars, because inactive behavior could be a refuge from predation, active behavior could represent both exposure to predation and escape capabilities.

The second group of behavior observations consisted of swimming speeds and distances of swimming when undisturbed (U) and disturbed (D). Swimming speeds as centimetres per second and swimming distances as centimetres were recorded by videotaping three larvae of each instar over a 1-cm spaced grid for at least 5 min of undisturbed and 5 min disturbed swimming. Disturbance was created by pipette pursuit. Six records of each individual were clocked twice by video playback as seconds and centimetres distance of swimming. For each individual there were six averaged records of swimming speed undisturbed (SSU), swimming speed disturbed (SSD), swimming distance undisturbed (CMU), and swimming distance disturbed (CMD). For each instar, comparisons of SSU to SSD, and CMU to CMD were made using ANOVA with a subjects x trials design with treatments fixed and blocks (individuals) random. Contrasts were made comparing instars I and II, instars III and IV, instars I + II versus III + IV, and I versus all three, for all four behaviors separately (SSU, SSD, CMU, and CMD).

Results

Aedes and *Chaoborus* Sizes and Field Densities

The four larval instars of *Aedes vexans* have a short aquatic phase with a gradual increase in body length (BL) during development and a saltatory increase in head capsule width (HC) after each molt. Both dimensions could have effects on predation rates by a gape-limited predator. Temperature strongly affects the life cycle length, including growth rates; development time is doubled at 18 versus 26°C. At 17.8°C, *Aedes vexans* (referred to hereafter as *Aedes*) will reach the median adult stage in 16 d, at 25.8°C in 7.7 d. At 17.8°C it will achieve median instar IV in 7.5 d, at 25.8°C in 3.7 d (N. Read, pers. comm.). In these experiments, *Aedes* reached instar IV body length of 6 mm in 3.3 d at 26°C and 7.9 d at 18°C. No significant differences within instars in BL or HC occurred between 18 and 26°C, but Brust (1967) did observe greater dry weights by instar at his lowest temperature of 21°C (see Table 7 for his weights at 21 and 26°C). Dry weights for instar IV averaged 0.366 mg (SD 0.133, $n = 10$), and for instar I 0.00683 (SD 0.000469, $n = 3$ sets of 30), comparable with those obtained by Brust (1967).

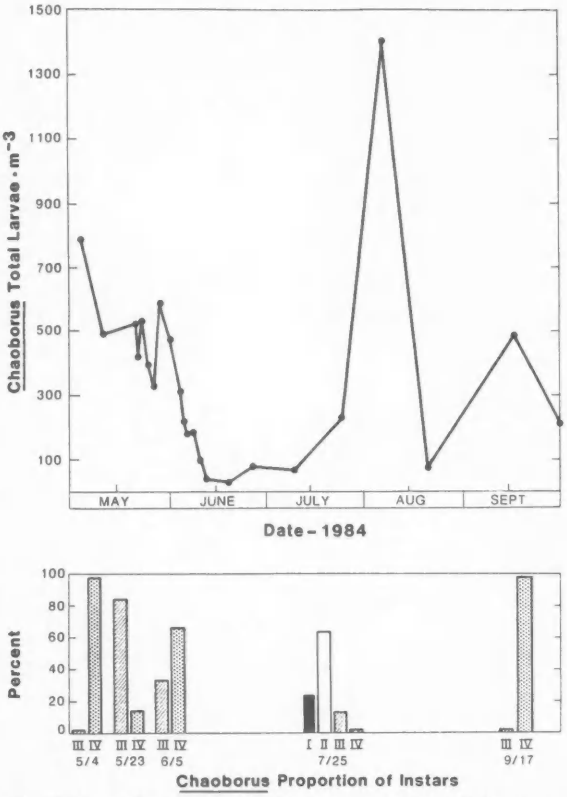

FIG. 1. Population changes in *Chaoborus americanus* in larvae per cubic metre and instar composition in percent from a pond in the Crow Hassan Park Reserve, Hennepin County, MN.

Chaoborus americanus differs dramatically from *Aedes* in having a long aquatic larval phase. In Minnesota, the midsummer cohort may develop to instar IV in early fall, and overwinter as larvae in shallow ponds, developing to adults in late spring (Fig. 1). Both instar III and IV are present from August through the following June. Instar IV larvae achieve an average body length of 11.1 mm and mouth gape, measured at the base of the mandibles, of 0.61 mm (Table 1). Estimates of field densities of instar IV *Chaoborus* (Helgen et al. 1988)

TABLE 1. Average gape diameters ($\bar{X}$) of species of *Chaoborus* and head capsule widths (HC) of larval *Aedes vexans* (*Aedes*) in millimetres by instar. CP = *C. punctipennis*, CA = *C. americanus*, CT = *C. trivittatus*. For CP, CA, and CT, $n = 30$.

	CP[a]		CA[b]		CA[c]		CT[b]		*Aedes*[c] HC	
Instar	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
I	0.126	0.006	—		—		—		0.327	0.0264
II	0.201	0.014	0.30	0.02	0.203	0.026	0.36	0.03	0.544	0.0235
III	0.332	0.019	0.43	0.04	0.328	0.0095	0.51	0.05	0.844	0.0195
IV	0.449	0.023	0.71	0.06	0.613	0.036	0.85	0.07	1.13	0.0388

[a]CP, Moore 1986.
[b]CA, CT Fedorenko 1975.
[c]CA, *Aedes* this paper, $n = 5, 8, 10$ for instars II, III, and IV, respectively.
BL = 4.3, 6.4, 11.1 mm for II, III, and IV, respectively.

indicate an approximate density range of 0.1 to 1·L^{-1} may occur in the spring.

Chaoborus Growth on *Aedes* or *Daphnia* Diets

Chaoborus fed instar I *Aedes* grew as well or better than those fed juvenile *Daphnia pulex*, at both 18 and 26°C (Fig. 2). The daily diets were in excess on 89.2% of 508 individual feeding days with *Daphnia* and 71.2% of 556 days with mosquitoes. There were no significant differences ($p > 0.05$) in initial body lengths among the four experimental groups by instar. In all cases, *Chaoborus* mean final instar IV sizes and growth increments were greater with the *Aedes* diet than the *Daphnia* diet, whether begun at instar III or IV, at 18 or 26°C. The differences were greater at 18 than 26°C. At 18°C, *Chaoborus* fed *Aedes* tended to pupate just a little later than those fed *Daphnia*, whereas at 26°C, those fed *Daphnia* pupated considerably later (10 d) than those fed *Aedes*. Student's *t* test comparisons of differences between the means of growth increments and pupation times of diet within each temperature are not statistically significant ($p > 0.05$).

Chaoborus Predation on *Aedes*

Predation rates determined by 16–17 h trials definitely vary with the instar of *Aedes* used as well as with the density of the *Aedes* prey (Fig. 3). Twenty-four hour predation rates at differing prey densities for instar IV *Chaoborus* range from 11–25 instar I *Aedes* consumed per *Chaoborus* to near 0.12 for instar IV *Aedes* (Table 2). Surprisingly, instar III *Chaoborus*, with a mouth gape of only 0.33 mm, consumed instar II and III *Aedes* (BL 2.8, 4.6 mm, respectively, HC 0.55, 0.83 mm, respectively) at rates close to those observed with instar IV *Chaoborus*. *Daphnia pulex* (0.84 mm) were consumed at 11–12 per day, fewer than the larger (1.8 mm BL) *Aedes* instar I larvae. There appears to be little difference caused by temperature in predation rates at comparable prey densities.

Prey density affects the predation rate as a different functional response for the three *Aedes* instars tested (Fig. 3). Increasing the density of an instar I prey results in an increase in the 2-h predation rate, with no saturation response appearing by 64 *Aedes* per litre. With *Aedes* II and III, however, a possible saturation appears at the 2 h predation of 4.5–5 *Aedes* per *Chaoborus* for *Aedes* II at around 10–30·L^{-1}, and a 2-h rate of 1.

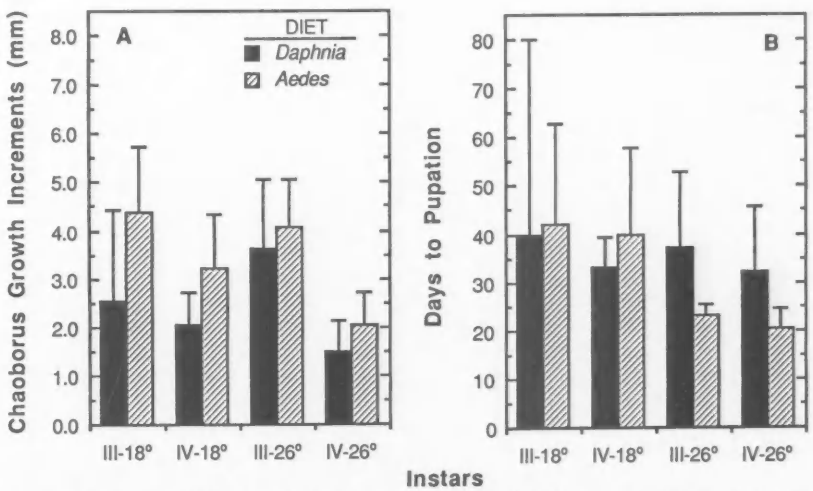

FIG. 2. Effects of a diet of instar I *Aedes vexans* or prereproductive *Daphnia pulex* on growth and time to pupation of *Chaoborus americanus*, with 95% confidence intervals. Growth increments = millimetres of growth from initiation of the experiment to the day prior to pupation. Initial lengths were not significantly different. Instars = initial instar of the *Chaoborus*.

TABLE 2. Average *Chaoborus* predation rates ($\bar{X}$) on larval *Aedes vexans* at different stages, and on *Daphnia pulex*. Average rates as numbers of prey consumed per *Chaoborus* in 24 h. Larval mosquito density or *Daphnia* densities (PD = prey density) as number per litre in parenthesis. Experiments actually run 16–17 h. *n* = numbers of *Chaoborus* tested.

		Aedes instars											
		I			II			III			IV		
Chaoborus instar	Temp (°C)	*n*	$\bar{X}$	PD	*n*	$\bar{X}$	PD	*n*	$\bar{X}$	PD	*n*	$\bar{X}$	PD
CIII	26	9	8.29	(20)	12	8.34[a]	(26.7)	5	1.43[b]	(26.7)		—	
								7	0.83[c]	(26.7)			
CIV	26	8	10.85	(18.7)	5	7.91	(9.3)	3	1.88	(4)	11	0.132	(10.7)
		9	23.79	(26.7)	8	8.61	(13.3)	5	1.43[b]	(26.7)		—	
		9	19.72	(33.3)	9	7.67	(13.3)	4	1.09[c]	(26.7)		—	
			—		8	9.28	(13.3)		—			—	
CIV	18	10	18.40	(26.7)	9	7.34	(13.3)		—		9	0.111	(10.7)
		7	25.35	(26.7)	9	5.34	(13.3)		—			—	
Daphnia as prey													
CIV	26	12	11.0[d]	(26.7)									
CIV	18	11	12.0[d]	(26.7)									

[a]50% MI and MII at end of experiment.
[b]10% MII, 90% MIII et end of experiment.
[c]40% MIII, 59% MIV at end of experiment.
[d]*Daphnia* $\bar{X}$ body length 0.836 mm (SD 0.0691), tail spine length 0.169 mm (SD 0.0296).

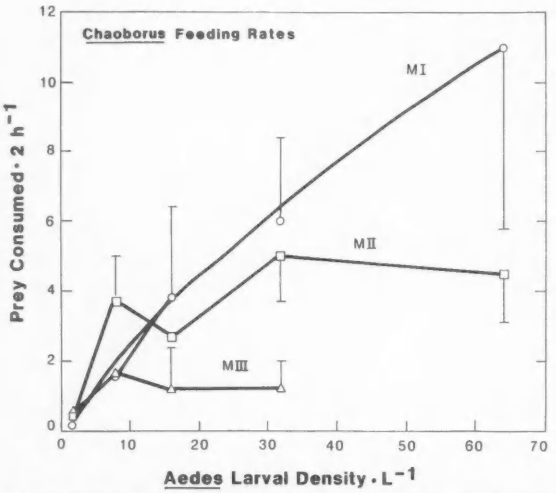

FIG. 3. Feeding rates of *Chaoborus americanus* on various densities of larval *Aedes vexans*: M_I = instar I, M_{II} = instar II, M_{III} = instar III. Predation rates shown for 2-h trials. *Chaoborus* density at $1.33 \cdot L^{-1}$, *Aedes* at 1.33 to $64 \cdot L^{-1}$. Actual volume used, 750 mL.

to 1.5 for *Aedes* III at $8 \cdot L^{-1}$. This 2-h rate on *Aedes* III is comparable with the 24-h rate (Table 2), suggesting satiation may be occurring.

Ingestion times (Table 3) increase strongly for each *Aedes* instar. Instar I is ingested almost instantaneously, in less than 1 s, while ingestion of instar II takes 6.3 s, III takes 366 s, and two observations of incomplete ingestions of instar IV ran at least 4800 and 10 800 s. Complete ingestion of instar IV was observed on several other occasions when ingestion times were not recorded. Using these ingestion times to calculate prey value, where prey value = weight (micrograms)/ingestion time (seconds) (Moore 1986) gives prey values for *Aedes* I of 15.1; II, 7.3; III, 0.68; IV, 0.12, and 0.053. Weights used are 21°C mid-instar dry weights derived from Brust (1967), see Table 7.

TABLE 3. Ingestion times ($\bar{X}$) (in seconds) of *Aedes vexans* larvae by fourth instar *Chaoborus americanus*. Ingestion times as seconds. *n* = number of *Chaoborus* tested.

Aedes instar	Ingestion times $\bar{X}$	SD	*n*
I	0.78[a]	0.506	13
II	6.30[b]	3.452	7
III	366	319.8	11
IV	one head capsule still exposed at 10 800 s after ingestion one head still exposed at 4800 s		

[a]A second ingestion soon after a first took 11.63 s.
[b]Inclusion of two second instar mosquitoes ingested head first alters $\bar{X}$ to 12.52 s (SD 13.081, $n = 9$). These ingestions were substantially longer (40.48 and 20.16 s).

Strike efficiencies as percent of attacks on *Aedes* I resulting in an ingestion from two experiments were 71% (24 strikes, 17 captures) and 69% (35 strikes, 24 captures). No determinations were made on instars II–IV.

Chaoborus instar IV, when given a choice of *Aedes* or *Daphnia* juveniles in equal numbers, strongly preferred *Aedes* instars I, II, or III, but not instar IV (Table 4). In 2-h trials with replacement of consumed prey, the preference for *Aedes* I, II, and III over *Daphnia* ranged from 66–86%, whereas only 13% of the time was instar IV taken over *Daphnia*. Interestingly, *Chaoborus* instar III's preference for *Aedes* over *Daphnia* was even stronger, 94–100%. The average body length of the *Daphnia*, 0.76 mm, was smaller than that of instar I *Aedes*, 1.8 mm.

Mosquito Behavior Results

Overall, the 10-min behavior records (Table 5) show *Aedes* larvae spend more of their activity time browsing than suspended for respiration at the surface with the respiratory siphon. ANOVA comparison of instars I + II versus III + IV for all

TABLE 4. *Chaoborus* prey choice experiments results, with numbers of *Aedes vexans* larvae (M) and *Daphnia pulex* (D) eaten when presented to *Chaoborus* (C) in equal numbers. M/(M + D) represents proportion of mosquito larvae chosen. n = number of *Chaoborus* tested.

C instar	M instar	Experiment (h)	M eaten		D eaten		M
			$\bar{X}$	SD, n	$\bar{X}$	SD, n	M+D
IV	I	17	16.7	3.44,11	8.55	3.83,11	0.66
IV	I	2	4.8	2.79,6	1.3	1.21,6	0.78
IV	II	2	2.9	1.54,17	0.77[a]	0.562,17	0.79
IV	II	2	2.0	1.0,3	0.67	1.15,3	0.75
IV	II	2	1.7	1.03,6	0.83[b]	0.753,6	0.67
IV	III	2	1.0	0.632,6	0.17	0.408,6	0.86
IV	IV	2	0.2	0.447,5	1.4	0.548,5	0.13
III	I	2	2.5	0.548,6	0.17	0.408,6	0.94
III	II	2	1.0	0.817,4	0	0,4	1.00

[a]*Daphnia* body length $\bar{X}$ 0.763 mm (SD 0.1348, n = 24).
[b]*Daphnia* body length $\bar{X}$ 0.764 mm (SD 0.1199, n = 13).

five behaviors in Table 5 was significant ($p = 0.025$) only for browsing and suspend at bottom ($p = 0.031$). Comparisons for all five behaviors of instar I versus II, III versus IV, and I versus all three were not significant. Similar ANOVA comparisons of instars for combined "active" behaviors (W, SC, B) with "inactive" (S, SB) showed a significant difference only for active behaviors for I + II versus III + IV ($p = 0.033$). Most of the active difference is brought about by the greater browsing in I and II.

Swimming speeds videorecorded showed linear increases by instar for undisturbed (U) and greater increases when the larvae were disturbed (D), especially in the older instars (Fig. 4A). Swimming speeds ranged from 0.6 to 2.0 $cm \cdot s^{-1}$ for instars I–IV, and maxima by instar order were 0.7, 1.2, 1.6, and 2.5 $cm \cdot s^{-1}$, respectively. Swimming distances in disturbed larvae increased with instar, most strongly with instar IV (Fig. 4B) as might be expected. The swimming distance response to disturbance (CMD) was not expected; instars I and II swam significantly ($p < 0.05$) shorter distances when CMD than undisturbed (CMU). Averages of CMU versus CMD for instar I were 3.5 versus 2.1 cm, respectively; instar II averaged 4.5 versus 2.8 cm distance. ANOVA comparisons of swimming speeds (U versus D) and of swimming distances (U versus D) for each instar were significant at the 0.05 level only for CMU versus CMD for instar I and instar II.

The reduced swimming distances in response to perturbation by instars I and II related to their very different behavior from that of instars III and IV. The latter, when disturbed, swam rapidly away from the disturbance source. In sharp contrast, instars I and II almost always swam to what appeared to be the darkest point, whether or not the disturbance source was in its path. Rarely did they respond and just swim away. Often they swam right into or around the pipet, even if it was "attacking" them. The negative phototactic response stimulated by the disturbance could not be overridden by the disturbance itself. Third and fourth instars, by contrast, showed a straight escape

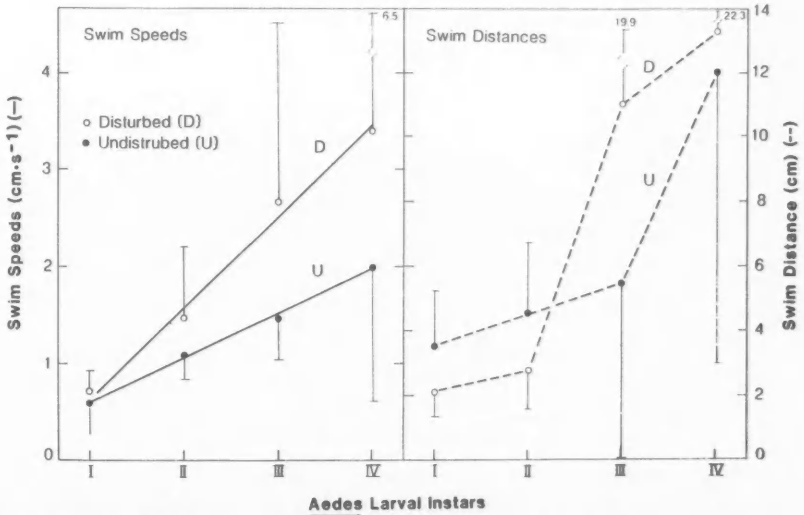

FIG. 4. (A) Swimming speeds in centimetres per second of the four larval instars of *Aedes vexans* undisturbed (U) and disturbed (D), and (B) swimming distances in centimetres per swim, with 95% confidence intervals.

TABLE 5. Larval mosquito (*Aedes vexans*) behaviors recorded in 10-min intervals as average seconds for *n* individuals of each larval instar. Behaviors, W = wiggle, SC = suspend cruise, B = browse, S = suspend, SB = suspend at bottom.

		W		SC		B[a]		S		SB[a]	
Instar	*n*	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
I	6	51.0	13.9	59.8	42.4	284.0	86.0	138.1	55.8	2.1	2.1
II	7	73.3	26.4	43.7	22.1	268.7	76.9	167.3	50.4	0.66	0.43
III	4	36.3	13.9	140.7	70.0	99.9	41.5	162.0	65.1	38.4	38.4
IV	6	41.3	18.0	59.2	18.9	108.3	35.1	270.3	41.5	31.1	11.1

[a]Anova (one way) significant difference between MI and MII versus MIII and MIV, $p = 0.025$ for browsing, $p = 0.031$ for suspend at bottom.

TABLE 6. Averages of larval mosquito (*Aedes vexans*) behaviors recorded in 10-min intervals as total seconds active (W + SC + B) and inactive (S + SB). See Table 5. Behaviors, W = wiggle, SC = suspend cruise, B = browse, S = suspend, SB = suspend at bottom. A greater number implies a greater vulnerability to predation.

		Active (W, SC, B)		Inactive (S, SB)	
Instar	*n*	$\bar{X}$	SE	$\bar{X}$	SE
I	6	394.8	57.1	140.1	54.9
II	7	385.7	55.6	168.0	50.2
III	4	276.9	106.5	200.4	90.4
IV	6	208.8	46.5	301.4	38.7

response and rarely a negative phototactic response to disturbance.

Prey Vulnerabilities

An index of prey vulnerability, v_r, is calculated using the undisturbed swimming speed (SS, centimetres per second) and reciprocal ingestion time (1/I, in seconds), on the assumptions that an increase in swimming speed increases the encounter frequency with a stationary predator, and therefore the vulnerability (Pastorak 1981), and an increase in ingestion time will reduce vulnerability. The undisturbed swimming speed was used because the mosquito larvae swam in their "undisturbed" mode around the immobile *Chaoborus*,

$$v_r = \mathrm{SS} \cdot \frac{1}{\mathrm{I}}$$

Pastorak's function, $v_x = \epsilon_x s_x$, requires the measurement of encounter frequencies (ϵ_x) and strike efficiencies (s_x) for all four instars. This is a better index of prey vulnerability than v_r, because strike efficiency includes successful prey contact and handling. However, data on strike efficiency for mosquito instars II–IV are not available. Prey vulnerabilities for *Daphnia* were calculated using the range of swimming speed values of 0.06–0.19 $\mathrm{cm \cdot s^{-1}}$ for *Daphnia galeata* (Gerritsen 1980), and *Chaoborus* handling times for *D. pulicaria* of 15, 20, and 190 s for 0.8, 1.0, and 1.8 mm body lengths (Pastorak 1981; Swift and Federenko 1975). It is expected the v_r or v_x values for *Daphnia* will be modified when size-specific swimming speeds are available.

The results show greatest vulnerability for *Aedes* instars I and II, and within *Aedes*, a sharp drop in vulnerability at instars III and IV. The vulnerability of even the smallest (0.8 mm) *Daphnia* is closest to that of the large active third and fourth instar *Aedes* larvae.

TABLE 7. Predation rates by *Chaoborus* (C) translated to equivalent numbers of instar I *Aedes* using 21° mid-instar dry weights from Brust (1967). 24-h predation rates from Table 2.

Aedes	Dry weight (mg)		Instar I	No. eaten by C in	*Aedes* I equivalents
instar	26.5°C	21°C	equivalents	24 h	eaten
I	0.0087	0.0118	1.0	11.0	11.0
				20.0	20.0
				24.0	24.0
II	0.038	0.046	3.9	7.7	30.0
				7.9	30.8
				8.6	33.5
				8.3	32.4
III	0.173	0.248	21.0	1.1	23.1
				1.4	29.4
				1.9	39.9
IV	0.472	0.576	48.8	0.111	5.4
				0.132	6.4

Discussion

The data presented here show that *Chaoborus* can profit from consumption of *Aedes* I, II, and III instars, and could potentially reduce *Aedes* populations where the species overlap, for instance in shallow semi-permanent ponds containing overwintering *Chaoborus* IV and *Aedes* eggs flooded at the margins in the spring. The prediction of a strong *Chaoborus* impact on *Aedes* larvae is based on its very high predation and rapid ingestion rates on the first two instars. In addition, *Chaoborus* prefers *Aedes* I, II, and III over *Daphnia* in choice experiments. The calculated prey vulnerabilities, based on swimming speeds and reciprocal ingestion times, indicate a distinctly greater vulnerability for *Aedes* I and II than for either *Daphnia* or *Aedes* III and IV.

The strike efficiency of 70% for *Chaoborus* on 1.8-mm instar I *Aedes* is much greater than that recorded on *Daphnia*, e.g. 15% for 1.9-mm *Daphnia* (Swift and Fedorenko 1975). It is well established that strike efficiency declines with zooplankton size, ranging from 43% for 0.6 mm *Daphnia* to 0% for 2.4 mm *Daphnia* for *C. trivittatus*, and from 25% to 0 for *C. americanus* (Swift and Fedorenko 1975). Although the strike efficiency on instar II *Aedes* isn't known, averages of 8–9 instar II larvae (BL 2.8 mm) were ingested per day, so it may be quite high.

The mosquito head capsule, while it may impede ingestion, does not set the limit on the size of prey eaten by *Chaoborus*. Within a mouth gape of 0.613 mm in instar IV, *C. americanus*

easily consumes *Aedes* I and II (head capsules 0.33, 0.54 mm, respectively), takes instar III with HC 0.84 mm more slowly, and occasionally eats instar IV, HC 1.13 mm. That instar III *Chaoborus*, with a gape of only 0.33 mm, can consume any instar III *Aedes* and a good number of instar II is remarkable. With greater gapes of 0.85 and 0.51 mm for instars IV and III (Fedorenko 1975), *C. trivittatus* would also be expected to prey strongly on *Aedes*.

Even with the lower predation rates on *Aedes* instars II and III, *Chaoborus* profits. The numbers of *Aedes* I equivalents, calculated from the determined predation rates on instars II and III and the mid-interval dry weights (Table 7), are greater with instars II and III as prey; the averages are 31.6 equivalents for instar II and 30.8 for instar III. The actual predation rate on instar I is 11–24 per *Chaoborus* per day. That is, it pays *Chaoborus* to ingest instars II and III, even at the low rate of 1.1–1.9 instar III per day. Since *Chaoborus* is only efficient at capturing smaller *Daphnia* it clearly has much to gain in taking larger-bodied prey that are easier to capture.

The results of the growth experiment, where diets of either *Aedes* I or small *Daphnia* were provided, are consistent with the observation of James and Smith (1958) that *Chaoborus* fed *Daphnia* took longer to pupate, although the results here were not significant. It is as if *Aedes* tends to promote growth at 18°C and shorten time to pupation at 26°C. This effect, if real, may be explained on an energetics basis. Estimated individual dry weights for 0.8-mm *D. pulex* (Edmondson 1955) and first instar *A. vexans* grown at two temperatures (Brust 1967) are 0.0047 mg and 0.0087–0.0118 mg, respectively. Based on the daily predation rates observed here, *Chaoborus* was consuming around 0.054 mg *Daphnia* per day and 0.160–0.300 mg *Aedes* per day using predation rates on *Aedes* of 18.4–25.4 per day, and 0.095 mg *Aedes* per day at the minimum observed predation rate of $10.9 \cdot d^{-1}$. This means, at the least, *Chaoborus* was ingesting twice the biomass with the *Aedes* diet as with *Daphnia*, and more likely 3–4 times the biomass. It should be noted that the *Chaoborus* had an excess diet of *Daphnia* almost all (89%) of the time and *Aedes* was in excess most (71%) of the time, so that the lower value of daily dry weight of *Daphnia* consumed was not caused by food limitation.

Some factors which will affect the degree of predation on *Aedes* by *Chaoborus* include water temperature effects on *Aedes* larval instar development time, larval density, larval size, and larval behaviors. The approximate doubling of the larval instar lifetime at 18°C means the time of exposure to predation is almost double compared with 26°C. Larval densities for *Aedes* will be affected by egg densities in the soils, by percent egg hatch, and by water levels when the wetland sites or pond margins are flooded. A typical average egg density of 0.60 $eggs \cdot cm^{-2}$ with a typical 50% egg hatch (N. Read, unpubl. data) would result in very different larval densities under different water levels, e.g. at 2 cm, 145; at 10 cm, 14.5; at 20 cm, 7.3 instar $I \cdot L^{-1}$, respectively. As demonstrated here, larval density, especially of instar I *Aedes* strongly affects predation rates. Information on *Aedes* larval densities is needed in order to predict whether *Chaoborus* predation could eliminate *Aedes*. This impact is not as great for instars II and III because of the saturation feeding response seen, probably related to the slower ingestion times and satiation.

Aedes swimming speeds and larval behaviors most likely affect its vulnerability to predation. The greater swimming speed of *Aedes* instar I, 0.6 $cm \cdot s^{-1}$, compared with that of *Daphnia*, 0.15 $cm \cdot s^{-1}$ (Riessen 1984) or 0.06–0.19 $cm \cdot s^{-1}$ (Gerritsen 1980), would certainly increase the encounter probability for *Aedes* with *Chaoborus*. *Aedes* instars III and IV exhibited greater undisturbed swimming speeds, 1.5 and 2.0 $cm \cdot s^{-1}$ than instars I and II, 0.6 and 1.1 $cm \cdot s^{-1}$, as well as swimming distances, which means encounter rates with sit-and-wait predators would be expected to increase with each *Aedes* instar. The significantly greater percent time spent in "active" behaviors by instars I and II could act to increase, and the greater percent time spent in inactive behaviors by instars III and IV could act to reduce their encounter frequency with *Chaoborus*. *Chaoborus* never attacked immobile *Aedes*. In deeper water, a browsing feeder like *Aedes* could be more vulnerable than in shallow water simply because of the greater transit needed from substrate to surface for air.

The escape response observed here by *Aedes* I and II to artificial disturbance is one of negative phototaxis and reduced swimming distance, a response not elicited by the immobile *Chaoborus*. Instars III and IV do not display their strong escape or "swim-away" response in the presence of immobile *Chaoborus*, but might when attacked. Further observations are needed. They are protected, presumably, by the greater ingestion times related to their larger size. It's also possible the greater speed, distance, and vigor of even "undisturbed" instars III and IV make attack, handling, and capture less likely even if the encounter frequency increases with the speed. The negative phototaxis for refuge-seeking in I and II, and the strong swim-away escape in III and IV may act to reduce vulnerability to active, nonambush type predators such as *Notonecta*.

The relative prey vulnerabilities calculated here using reciprocal ingestion times for all four *Aedes* instars indicate instar I is the most vulnerable; the greatest decline in vulnerability occurs between instars II and III where III is 44 times less vulnerable than II, which is 4.5 times less vulnerable than instar I. This major change in vulnerability between instars II and III is consistent with the data presented here on predation rates and behaviors, all of which suggests the first two instars of *Aedes vexans* are distinctly more vulnerable to *Chaoborus* predation than are instars III and IV. Analysis of prey vulnerability would be improved with data on *Chaoborus* strike efficiencies for all four *Aedes* instars, so that Pastorak's (1981) prey vulnerability function could be used. The reciprocal ingestion time used here is not a good indicator of the strike efficiencies needed because ingestion time does not include the probability of a strike or of an ingestion.

In conclusion, the greater vulnerability of *Aedes* instars I and II to *Chaoborus* predation can be explained on the basis of smaller size, more rapid ingestion times, and the lack of triggering of escape responses. *Aedes* larvae in instars I, II, and III are a profitable prey item for *Chaoborus*, even more so at lower temperatures because of greater *Aedes* body weights. *Chaoborus americanus*, then, is capable of ingesting a wide range of prey sizes, including not only fourth instar *Aedes vexans* (6.2 mm), but also other species of *Chaoborus* (von Ende 1982) and even its own during the cannibalistic incomplete ingestions seen here when IVth instar *C. americanus* were crowded. This predator, with its muscular crop, seems well adapted to ingest long-bodied prey like Dipteran larvae. *Chaoborus cooki* has even been suggested as a biological mosquito control agent (Borkent 1980) because of its diapausing egg.

It is entirely possible that predators like *Chaoborus* and *Notonecta* (Murdoch and Sih 1978; Sih 1986), with long aquatic larval life cycles and high predation rates, could have played a central role in driving *Aedes* to lay its eggs in very shallow,

temporary habitats. *Daphnia* co-exists successfully with *Chaoborus*; it has evolved a smooth, rounded transparent carapace, and undergoes predator-induced morphological changes like *Chaoborus*-induced neck-spines (Grant and Bayly 1981; Havel and Dodson 1984; Krueger and Dodson 1981) and cuticle thickening (S. I. Dodson, pers. comm.) as anti-predator adaptations. By the time *Daphnia* reach 2.0 mm body length and larger, they are essentially invulnerable to *Chaoborus* predation.

The hypothesis that prey that do not co-exist with a predator will be easier to capture than co-existing prey is supported by the data given here. *Chaoborus* preys more on *Aedes* and prefers *Aedes* over *Daphnia* which appear to be less vulnerable than both *Aedes* I and II. Even small-sized *Daphnia* have managed to reduce their vulnerability to the level of vulnerability for the large, active third and fourth instar *Aedes* larvae. Strike efficiency comparisons used to test this hypothesis may only be part of the analysis: overall predation rates, demonstrated prey preference for excluded prey, and measures of prey value in predator growth experiments may also be informative. In conclusion, *Chaoborus* is a potentially important predator on mosquito larvae, its impact on natural mosquito populations merits further study.

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